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Structure of the Lateral Line System of Macrones gulio

BY

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Zoology Research Laboratory, University of Madras

(Received for publication, October 20, 1959)

ABSTRACT

Observations on the histological structure of the lateral line system and its end-organ reported in this paper are preliminary to a series of behavioural and eletrophysiological experiments being performed on these fishes by the author. The skin of *Macrones gulio* was found to contain not only the lateral line receptors, but also the pit organs and gustoreceptors out of which the pit organs show a structure eminently suited for the perception of bare contact stimuli whereas the lateral line receptors would be more appropriately suitable for the perception of vibrational stimuli.

(1) *Introduction*

A complete picture of the function of a sensory organ could be gained only through a study of the microscopic structure of the end-organs as well as a study of the responses evoked by external stimuli. Except Katsuki, Yoshino and Chen (1950, 51) and Katsuki and Yoshino (1952) all the previous authors who had studied the function of the lateral line organs either by behavioral experiments or electrophysiological experiments have not related their findings to any feature of structure of these organs. The incompleteness of such a purely experimental approach would be obvious from the fact that a few of them, eg. von Frisch and Stetter (1932) and their associates, have ascribed the perception of sound stimuli they could not relate to the ear, to the skin. What type of sensory organs in the skin of the fishes they studied would be responsible for this specialiazed function is not clear.

Inasmuch as several workers who studied "hearing in fishes" experimentally have ascribed a certain role to the skin or to the lateral line organs, a composite sensory organ such as the skin, with different types of receptors, must be treated as a morphological unit. Previous work on cutaneous sense organs as

reviewed by Bhatti (1952) shows that the skin of fishes contains besides the lateral line end-organs, diffusely scattered pit organs gustoreceptors and epidermal cells and free nerve endings. The pit organs which are lodged in slight invaginations of the skin have been shown to be similar to the lateral line organs by earlier authors, i.e., Leidig (1851), Wright (1884), and also by Bhatti (1952). Some of these have even regarded them as accessory to the lateral line organs in function and have consequently treated them together as "Rheoreceptors" (Bhatti, 1952). The detailed structure of the lateral line organs of fishes and amphibia have been studied by several investigators. Of the more recent authors Denny (1937) has shown that the lateral line end organs of the teleost *Fundulus heteroclitus* consists of flask-shaped sensory cells with "hairs" imbedded in a gelatinous cupula and irregular supporting cells.

With regard to the innervation of the sensory cells of the lateral line end-organ, Bunker (1897) reported extracellular naked and free nerve terminations in *Ameiurus nebulosus* which Charippar (1928) and Chezar (1930) described these nerve endings as intracellular in the amphibians they had studied. On the other hand Johnson (1917) described knobbed nerve endings in *Mustelus canis*. Katsuki, Y., Yoshino, S. and Chen, J. (1951), the only authors who have attempted to interpret the results of experiments on lateral line organs in relation to their histology, found that the lateral line nerve consists of both thick as well as thin fibres and that the former innervate the central part of the sensory unit while the latter supply more peripheral cells. These authors have shown experimentally that the thick fibres indicate greater synchronised activity when the end-organs are simulated by sounds of low frequency, whereas the thin fibres show resting discharges in a more marked way.

In the present paper, the details of structure of the pit organs and the lateral line sensory unit of *Macrones gulio* are reported.

(2) *Material and Methods*

Fresh fish were pithed and the skin and tissues around the entire length of the lateral line was removed with the nerve and fixed in 4% saline formol. Paraffin and celloidin serial sections were made and stained in Mallory's triple. Silver impregnation method as modified by Peters (1954) was employed for a special study of the nerve endings. Impregnating the sections at pH of

6·8 was found satisfactory. Since the cupula suffered damage during the above procedures, fresh frozen sections of the lateral line were made and examined by phase contrast microscopy.

Reconstructions of the course of the lateral line canal and the pore canals were made from the serial sections.

(3) *Structure*

The Skin Receptors.

Transverse sections of the skin reveal that the skin in this fish is composed of two layers i.e. the outer epidermis and the inner dermis or corium. The entire epidermis is made up of several layers of cubical and rounded cells with large mucus cells interspersed between. The pit organs may be distinguished as shallow pits bearing a group of specialized cells (vide infra.). Below the epidermis lies the subepidermal nerve plexus and free nerve endings.

(i) *Pit organs.*

The pit organs are pear-shaped and consist of a bulbous cupula fitted into a shallow depression in the epidermis 30 μ to 50 μ in diameter. They occur scattered on the flanks, above and below the level of the lateral line (Text-fig. 3). The specialised epidermal cells lining the pit are of two types, the sensory cells and the supporting cells. The supporting cells form the edges of the pit while the sensory cells form the base. The sensory cells are club-shaped with pointed apices, resting on which is the lower surface of the cupula. This appears to be (Text-fig. 3) a solid mass of mucus, bulb-like in form whose narrow blunt tip projects beyond the general skin surface. From the form of the cupula and its relationship with the socket-like depression it appears probable that this endorgan is capable of receiving contact stimuli like touch, pressure, or stroking and transmit them to the sensory cells at its base. Hence this mass of mucus described as cupula is likely to function more like the encapsulated club-shaped pacinian body rather than the loose gelatinous mass of mucus described as cupula terminalis occurring in the labyrinth, (Katsuki and Yoshino, C.J., 1951). As has been the experience of Bhatti (1952) also different methods employed by the author including silver impregnation technique failed to differentiate the nerve terminations in the pit organ. It is very probable that these are innervated by twigs from the lateral line nerve as has been suggested by Ewart (1892) and Herrick (1903). This probability is increas-

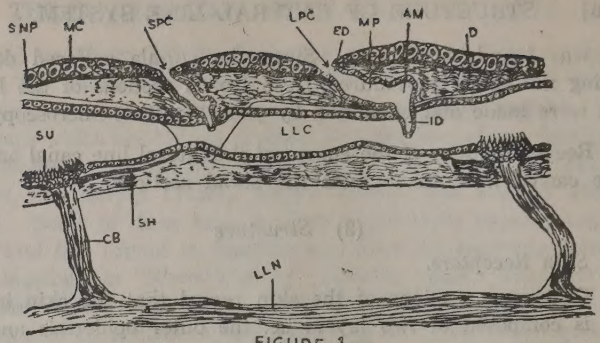

FIGURE 1

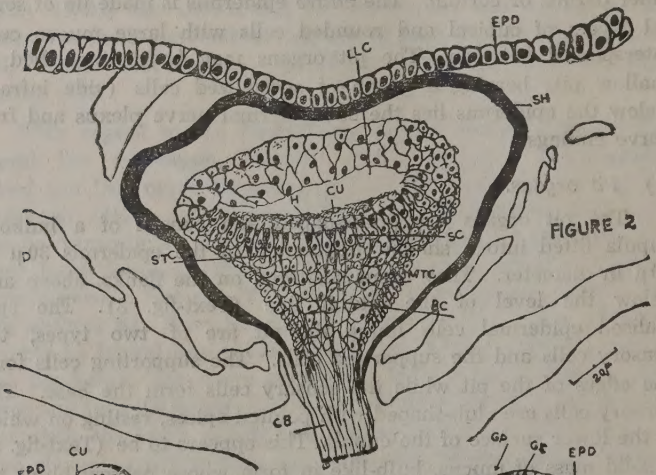

FIGURE 2

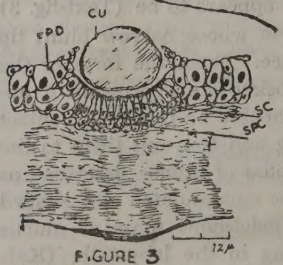

FIGURE 3

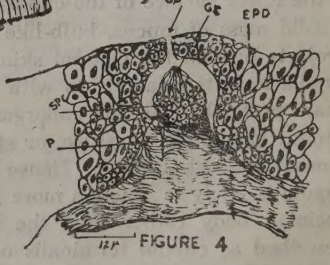

FIGURE 4

Text Figs. 1-4: Fig. 1. Figure showing two segments of the lateral line canal and the various parts of the pore canal; Fig. 2. Detailed structure of a single lateral line end-organ; Fig. 3. Microscopical structure of a pit organ; Fig. 4. Structure of a gustoreceptor.

AM Ampulla; BC Basal cells; CB Collateral bundle; CU Cupula; D Dermis; ED External duct; EPD Epidermis; GC Gustatory cells;

ed by the results of experimental stimulation of the skin reported in the earlier papers (in press) and also by the close proximity of the pit organs to the lateral line nerve trunk. It must be however mentioned that it is possible that the sub-epidermal nerve plexus which makes the entire epidermis sensitive may also offer spinal pathway for impulses.

(ii) *Gustoreceptors or taste buds* were also found in the skin (Text-fig. 4). They consisted of specialised sense cells with no cupula. The general disposition and character of the cells recall those of the taste buds and chemoreceptors. (Bhatti 1952). Each gustoreceptor is in the form of a bud resting on a papilla of the corium which at that region is raised in the form of a concial outward extension. This chemoreceptor which is contained in a vescicle opening outside through a pore consists of two types of cells. The spindle-shaped gustatory or neuroepithelial cells form the apex of the organ and their filamentous continuations form a tuft on the organ. The small rounded basal cells form the broad base of the organ. Such a structure as seen in the chemoreceptor is distinctly different from the pit organ in not showing a cupula and the regularly arranged sensory cells as would be seen in the lateral line end-organ (vide infra).

The Structure of the Lateral Line System.

The lateral line system in this fish may be considered in three sections i.e. (i) the pore canal system, (ii) the lateral line canal, and (iii) the lateral line sensory unit.

i. *Pore Canal System.* (Text-fig. 1)

Externally the skin bears a lateral row of pores which are of two sizes, i.e. large and small alternating with each other. They lead down into pore canals which penetrate through the outer epidermis as well as the plexiform nervous layer and the lateral line canal which runs through the fibrous connective tissue. Each pore canal consists of an external duct (ED), a middle part (MP) with an ampulla (AM) and an internal duct (ID) (see Fig). The entire pore canal is lined by columnar or conical cells with large nuclei. The canal is obviously epidermal in origin. The pore

GP Gustatory pore; H 'Hairs'; LLC Lateral line canal; LLN Lateral line nerve; LPC Large pore canal; MTC Mantle cells; P Papilla; SC Sensory cells; SH Sheath; SPC Supporting cells; SU Sensory Unit; SPC Small Pore canal; SNP Sub epidermal nerve plexus; STC Sustentacular cells.

canals leading from the smaller pores have smaller ampullae lined by rounded cells. The internal ducts are also shorter. Consisting of these three parts, each pore canal is so tortuous in its course that though outside water may fill it partially, a free flow into and out of it is improbable.

ii. *The lateral line canal* (Text-fig. 1)

The course of the lateral line canal is indicated externally by a lateral line running from the operculum to the beginning of the caudal fin. The lateral line canal lies at the inner ends of the pore canals and has a moniliform outline being dilated behind the junctions of the canals from the large pores. Within this dilation the inner wall shows a specialized group of cells constituting the lateral line sensory organ. The rest of the wall of the canal is of small rounded cells. This longitudinal canal is enveloped by a sheath composed of layers of secretion from the surrounding connective tissue. It is interesting to note that only the large pore segments bear the sensory units. Bhatti (1952) who has described the lateral line system in a siluroid *Rita rita* has not reported these large pore segments being different from the small pore segments which do not contain the sensory unit.

iii. *Lateral Line sensory unit* (end-organ)

The sensory organ occurs only in the dilated segments of the canal. It is made of four different types of cells i.e. sense cells, sustentacular cells, basal cells and mantle cells. The sense cells (SC) are flask-shaped and bear sensory hairs at their tips protruding into the lumen of the lateral line canal. Fresh frozen sections when examined through a phase ocntrast equipment reveal a gelatinous cupula within the lumen, resting on the sensory hairs. Study of the several serial sections show that the gelatinous mass is structureless and like the cupula or the mucoid mass described in the labyrinth has an irregular outline and has no definite form, The flask-shaped sense cells contain large ovoid nuclei at the base, and dark thread-like mitochondrial bodies in the neck region. The base of the cell is drawn out into a tail-like extension which mingles with the nerve plexus below. The rest of the sensory organs consists of the supporting cells i.e. the sutentacular cells which are thin and spindle-shaped lying between and below the sense cells. The basal cells (BE) are irregularly shaped packing cells forming the conical base of the end-organ. Between these packing cells run the nerve tails of the sense cells till they are

collected into the collateral bundle leaving the end-organ. The mantle cells (MTE) form the epithelim covering the base and extend over the sides of the lateral line canal. These are however so arranged as to admit the penetration of minute nerve fibres and blood vessels supplying the sense organs. In *Macrones gulio* the lateral line nerve trunk gives off at intervals collateral nerve bundles each of which enters a sensory unit through a foramen in the sheath covering the canal. The nerve fibres reach the sensory end-organ on the axial side and become continuous with the nerve tails of the sense cells. Examination under oil immersion shows dilated knob-like terminations of some of the fibres of of the collateral bundle, resting against the bases of the sense cells.

(4) *Remarks*

The skin of *Macrones gulio* shows two sets of sensory receptors i.e. the more superficial sensory units or the pit organs and the gustoresceptors, and the more complex system of lateral line organs consisting of the pore canals, the lateral line canals and the lateral line end-organs. The gustoreceptors are few on the sides of the body being more numerous nearer the mouth and barbels. The pit organs with the bulb-like solid mucoid body fitting into the epidermal sockets are eminently suited for receiving contact stimuli whereas the disposition of the lateral line system especially the end-organ recalls those of the labyrinth suggesting a similar function. However, further experimental proof would be required to relate the structure of this system of sense organs to the exact function they perform.

(5) *Acknowledgments*

I wish to thank Dr. C. P. Gnanamuthu, M.A., D.Sc., F.Z.S.. Director, University Zoological Research Laboratory for outlining the problem and for his unfailing guidance during the course of this work. My thanks are also due to Dr. S. Krishnaswamy, M.Sc., Ph.D., Reader of this department for his useful discussions.

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The Lateral Line System and Sound Perception in Catfish

BY

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ABSTRACT

Through a method of recording the simple unconditioned response of the fish to sound stimuli of accurately measured frequency and intensity simultaneously with the stimulating sound impulse, and a statistical analysis of the stimulus-response coincidences, inferences drawn regarding the frequency range of response and intensity threshold of sound perception of intact fishes, and fishes in which either the ear or the lateral line organs had been operatively eliminated are reported in this paper.

(1) *Introduction.*

As the early histological studies of Allis (1889), and Bunker (1897) made it clear that the lateral line organs must be of a sensory character, it stimulated several authors to determine experimentally its exact function. Hofer (1908) concluded that this system of sense organs should help the fish to perceive weak water currents. Dijkgraaf (1933) through a series of conditioned reflex experiments combined with the organ elimination technique, attributed a sense of 'Distant touch perception' to these organs. Based purely on electrophysiological experiments Hoagland (1935) concluded that these sense organs serve as temperature receptors to the fish, and even suggested that they may be concerned with a proprioceptive function.

Whether sound vibrations would form an appropriate stimulus to the lateral line organs has been investigated by several authors. Parker and Van Huesen (1917), as a result of elaborate ablation experiments and noting the response of the fish to sounds of different frequency i.e. 43,86,172,344,688,1376, and 2752 cps concluded that "there is no direct evidence of the lateral line acting as receptors", although they reported that whenever the lateral line was left intact in conjunction with either the skin or the ear, the percentage of responses of these fishes to sounds showed

a marked decrease when compared with the percentage of response of the intact fishes. They felt that the lateral line system produces only inhibitory impulses whereas the ear and and the skin produce excitory ones. This conclusion was further strengthened by the fact that when the ear and the skin were put out of commission and only the lateral line was left intact, the fishes did not evince any response. But their having made use of undetermined stimuli like "the impact of a leaden ball on the walls of the aquarium", and "slow vibratory movements of the whole body of water", and having made only visual observation of the behavioral responses make their conclusion not so acceptable as it otherwise will be.

In the course of electrophysiological studies of the lateral line nerve-end organ preparations oriented towards other related problems, Hoagland (1935), Suckling and Suckling (1950) and Katsuki *et al* (1950, 1951) showed that the lateral line system acted as receptors to sound vibrations under water though they did not pursue their investigations as to the possible share taken by the lateral line in the total sound perceptive capacity of the whole fish.

With regard to the hearing capacity of fishes, von Frisch and Stetter (1932), von Frisch (1938), Dijkgraff (1950, 1952) and Kleerekoper and Chagnon (1954) who experimentally studied this problem were preoccupied with the functions of the various parts of the ear (as the only hearing organ) and referred to all that could not be related to the ear as perceived by the skin as a whole—"cutaneous tactile perception" as held by Dijkgraaf (1933).

In the present account the results of experiments performed on the intact as well as ablated catfish *Macrones gulio* in order to determine their range and intensity thresholds using precisely determined sound vibrations of definite frequency and intensity as stimuli are reported. Electrophysiological studies on the response of the lateral line nerve end-organ preparation to under water sounds, are also being made and would be reported subsequently.

(2) *Material and Methods.*

Using a system of Audiooscillator and a high power amplifier, sounds of definite frequency and intensity were projected into water through a specially matched speaker unit to which a short polythene tube was firmly fixed and immersed in water 3 inches

below the surface. This assembly would radiate approximately spherical waves from the end of the polythene tube, and if the reflections from the flat surfaces of the aquarium are reduced to a minimum by covering them with soft fibre mesh blocks so that the radiated sound field is not affected by such reflections, the energy will be spread uniformly over a complete spherical surface at any radius from the source. Therefore the intensity will be related to the source power. Since this tube would give out spherical waves from its circular end and cylindrical waves from its radially pulsating length, the intensity of the sounds reaching the fish had to be definitely measured and checked with the help of a calibrated system of hydrophone (Massa M, 115·B), amplifier, and an output meter in terms of db above a reference level of 0·0002 dynes/sq. cm.

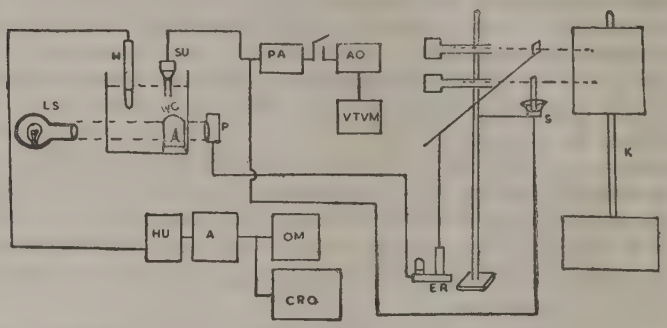
Short bursts of sounds of one or two seconds duration were administered through a noiseless tap-key type of switch. Sounds of certain frequencies, which suffered undue distortion as revealed by checking through an oscilloscope, were not used in the experiments.

Recording the response of the fish.

Since training the fish to associate feeding (reward) or shock (punishment) with sounds of selected frequency and intensity would not only limit the number of tests, but also would increase the number of other factors too complicated and difficult to analyze and interpret accurately, in the present experiments, it was felt that the simple bodily movements of the fish from a resting position coincident with a given sound stimulus may be accepted as response. The danger of the oversimplification of the reflex arc as a sort of inert conducting pathway beween receptors and effectors was however minimised by giving ten bursts of stimuli on each fish with interval of at least two minutes, the experiments being repeated on five different fishes in each case. Even the use of such simple unconditioned reflex was found to be of little use in fishes which are very sluggish by nature, or fish whose labyrinth had been ablated and which therefore were not able to swim freely and readily.

For each test the fish was taken afresh from the stock aquarium and enclosed in a thin wire mesh cage and placed within a glass tank enclosed in another larger tank and the spaces at the bottom and sides were packed with sponge rubber pads leav-

ing only a circular hole through which the light beam actuating the photoelectric cell was passed (Text-fig. 1).



TEXT FIG. 1

Experimental arrangement set up for the production and measurement of sound stimuli and recording of response of the fish. A, Amplifier; AO, Audio-oscillator; CRO, Cathode ray oscilloscope; ER, Electronic relay; H, Hydrophone; HU, Hydrophone power unit; K, Kymograph; LS, Light source; OM, Output meter; P, Photo cell; PA, Power amplifier; SU, Speaker unit; S, Speaker voice coil; VTVM, Vacuum tube volt meter; WC, Wire mesh cage.

The other extraneous sound disturbances were eliminated by conducting the experiments in a sound proof room and mounting the table on blocks of foam rubber. Since the room was adequately darkened, lit only by a photographic safe lamp, and the experimenter was behind a screen, visual distractions of the fish were reduced to a minimum. Under these conditions the fish usually remained resting within the enclosure unless agitated by the test sounds in response to which the fish made a jerky forward movement into the upper part of the tank with some effort. These response movements were recorded though the photoelectric electronic relay on photosensitive paper moved by a kymograph drum. In order to facilitate an easy analysis of the stimulus—response coincidence, the test sound was also recorded at the instant of administration on the same strip of paper through a parallel circuit actuating the voice coil of a speaker (Text-fig. 1).

All these experiments were repeated a number of times and the observations were subjected to statistical analysis. The data relating to the percentage of response to varying frequency suggested that exponential curves of the type $y = ab^x$ (where x stands for frequency, y for the percentage of response, and a and b are constants) can be fitted to them.

The constants a and b are obtained by solving the equations

$$n\,a + b\Sigma x = \Sigma \log y$$

and $$a\Sigma x\ b\Sigma x^2 = \Sigma x \log y$$

(n = No. of observations made).

Theoretical values of percentage of responses are estimated from the fitted equation. The observed and estimated percentage of responses have been plotted together (graphs 1 & 2). The fitted curve represented the trend of percentages of response in relation to frequency. From a comparison of this curve with that obtained through the observed values, it was possible to recognize wide fluctuations in the responses of the fish and errors due to sampling.

Experiments and results

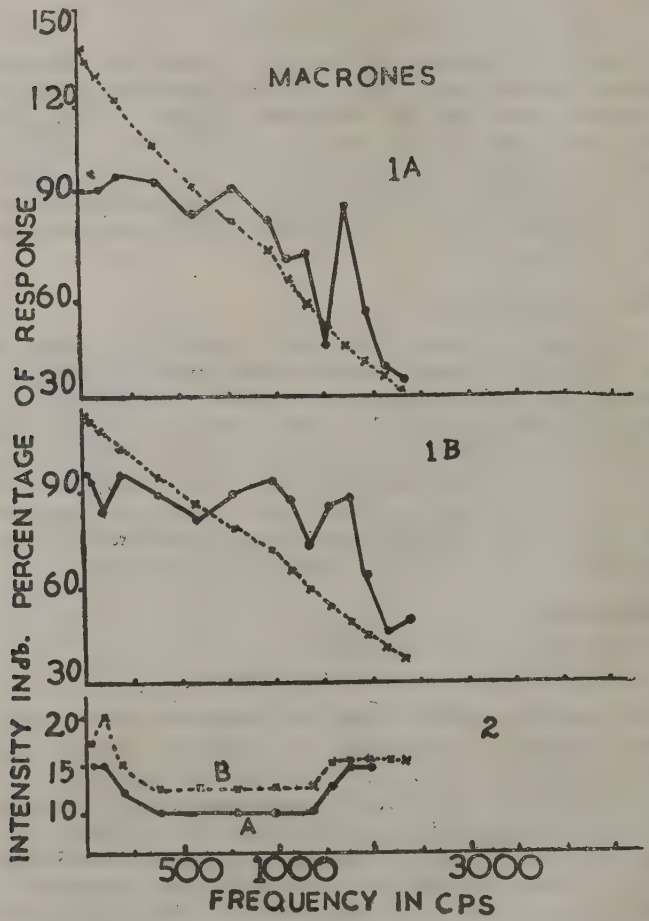
Two series of experiments were performed to determine (A) the frequency range of response and (B) the intensity thresholds at the various frequencies. In both the series (A & B) experiments were performed on fishes whose ear or the lateral organs had been operatively eliminated. Study of the histology of the skin of the catfish showed that only in this species, *Macrones* there were the pit organs. The detailed structure of these was such that the skin did not deserve separate consideration and no attempt was made to study its response to sound stimuli.

Macrones gulio

Experiment No. 1. Intact fishes.
Series (A) Frequency range of responses.

In these experiments aimed at determining the frequency range of response of normal fishes, the intensity of the stimulating tone was kept constant at a level of 20 db. above a reference level of 0·0002 dynes/sq.cm. Sound stimuli ranging from 15 cps. to 5000 cps. were applied in two series i.e. 15, 200, 400, 600, 800 etc. upto 5000, (200 cycles intervals), and later 40, 60, 100 and 150 cps. At each of these frequency levels ten applications were made on each of the five fishes. The number of stimulus-response coincidences was counted from the Kymograph for the fifty applications and was expressed as percentage of response of the fish to sounds at that frequency. The data so collected are illustrated by graph 1 A. It will be seen that there is 96% response to low frequency sounds and that as the frequency is raised to 2100 cps. the fish respond only on 50% of the occasions and to one in four

applications of sounds at 2400 cps. It may be inferred that the fish distinguishes sounds 200 cps. apart throughout its normal hearing range, i.e., from 15 cps. to 2100 cps.



GRAPH 1A Frequency range of response of intact fishes.

GRAPH 1B Frequency range of response of fishes with lateral line organs operatively eliminated.

——Observed value. - - - - Calculated value.

GRAPH 2. Intensity thresholds of sound perception

A Intact fishes. B Fishes with lateral line organs eliminated

Experiment No. 2. Fishes with only the ear intact

Each fish was anaesthetised by leaving it for 20 minutes in a bowl of 1/1000 solution of a fish anaesthetic (Sandoz MS. 222). The lateral line nerves on either side were cut across, care being taken to cause as little haemorrhage as possible. The cut ends of the nerves were gently pulled till the entire lengths were extracted. It was found that fish recovered from the anaesthetic in about 40 minutes and swam about and fed normally.

As in the former experiment No. 1 the percentage of responses of such fishes to sounds of different frequencies were noted and tabulated, and illustrated in graph 1B. A comparison of this graph with graph 1A will show that the ear left alone can perceive sounds of frequency higher than 2100 cps and that 50% responses are obtained even at 2400 cps. It will also be clear that throughout the entire range of hearing, the ear appears to be more sensitive, as indicated by higher percentages of response.

Experiment No. 3. Fishes in which the ear was put out of commission

Though several authors like Parker and Van Huesen (1917), Von Frisch (1938) and Dijkgraaf (1950) have performed experiments eliminating the ear, their published accounts do not give details of how complete such removal has been. A sharp incision was made dorsal to the otic region of anesthetised fish and the entire membranous labyrinth was removed in bits and the auditory nerve was severed with the help of a sharp needle. The wounds on both sides were plugged with cotton and covered with strips of plaster. When the fishes recovered from the effects of the anaesthetic, they fed when food was dropped within reach, but appeared sluggish, swimming in a clumsy way. Labyrinthectomy deranged its equilibrium to such an extent that the fish moved only when violently agitated; so much so that there were only 2% responses to any of the sound stimuli administered. It was realised that had the behavioral index been anything else than a quick swimming movement it would not have been vitiated by the removal of the semicircular canals of the ear. There was no way of retaining the semicircular canals and removing the acoustic parts of the ear alone.

Series B. Intensity thresholds at different frequency levels

In this second series of experiments the intensity of the stimulating sound was varied keeping the frequency constant and the threshold intensity needed for response was noted.

Experiment No. 4. Intact fishes

Since the purpose of this series of experiments was to determine the lowest threshold, stimulation was first commenced at 5 db in each case and then raised by steps of 2·5 db. After the tests at one frequency level the fish was retruned to the aquarium and another was taken. Thus five such fishes were tried at each frequency level allowing an interval of at least five minutes between two successive tests. The data so collected are shown in Table 2 and illustrated in the graph 2A. It will be obvious that in a large part of the audible range i.e. from 400 cps. to 1700 cps., the intensity has to be varied from 10 db to 12 db. Increasing the intensity to 15 db and to 18 db extends the lower part of the range to 100 cps. and 15 cps. Similarly increasing the intensity to 20 db extends the higher reaches to 2400 cps.

Experiment No. 5. Fishes with the ear alone in a functional condition

The lateral line system was eliminated in five fishes as in experiments No. 2. Sound stimuli of different frequencies were administered varying the intensity. The data of responses are presented in table No. 2 and graph No. 2B. It will be clear that as indicated by graph 1B as well as 2A increase of intensity of the sound stimulus renders sounds of frequency above 2100 cps. to 2400 cps. effective in inducing a 50% response and that the ear is responsible for this extension. It will also be clear that for the greater part of the range i.e. from 400 cps. to 1400 cps. a very low threshold of 10 db. is sufficient for the ear to perceive the stimuli, suggesting that higher thresholds in this range and lower thresholds below and above this range (see graph 2A) manifested in the intact fish are probably due to the interference or inhibition by the lateral line organs. This suggests that the lateral line organs react to sound stimuli in this way.

Experiment No. 6. Fishes in which the ear was ablated

The labyrinth was removed in five fishes by a procedure described for experiment No. 3. As in that experiment the fishes lost their control of their equilibrium and became more or less immobilised, the sporadic clumsy movements were too limited to be of any significance as behavioral responses. Hence, this inability to study the labyrinthectomised fishes was made good by the electrophysiological investigations reported in a succeeding paper.

(4) *Discussion*

The observations of previous authors regarding the perception of low frequency sounds by fishes are not very conclusive. Dijkgraaf (1950) while investigating the functions of the ear labyrinth removed *pars superior* in *Gobius paganellus* and found that the hearing was not affected. But when he removed the *pars inferior* the upper limit dropped from 800 to 500 cps. He claims to have obtained "clear reactions" at 100 cps., after eliminating the *pars superior* and organs of the lateral line as well. This response Dijkgraaf attributes to "cutaneous tactile perception" rather than to any other sensory organ. It is not clear how he rules out perception through the lateral line organs, for operative elimination of the whole system of lateral line organs without accessory damage to the tactile sense endings in the integument is not easy. von Frisch and Dijkgraaf (1935) found that *Phoxinus laevis* exhibited an orientation at short distances towards strong sound vibrations shaking the water. This was attributed by them to skin sense rather than to lateral line. Reinhardt (1935) experimenting on the same fish found "in some cases a positive perception of direction occurred when the fish was within a proximity of 10 to 20 cms. of the sound source". Since this response was detected even after the elimination of the lateral line system, ear, and Weberian ossicles, he attributed this reaction to the function of the skin sense.

On the other hand, all experimental evidence regarding perception by the lateral line organs amounts to mechanical stimuli of very low frequencies and of large intensities. Hofer (1908) conclusively showed that the lateral line helps perception of water jets directed periodically against the various regions of the lateral line system in *Esox lucinus*. Dijkgraaf (1933) proved that the lateral line system helps the fish to localize objects at a distance, "Ferntastsinn". "These objects may either be moving (prey or enemies) and thus constitute the focal point of a mechanical disturbance, or their presence and localization may be perceived and accurately computed from the time relations of reflected water waves set up by the swimming movements of the fish itself. The latter case would fundamentally conform with the principles of echo-location", (Lowenstein, 1957). Intermittent water jets, or a vibrating body under water, or water waves reflected from objects, all approximate to very low frequency vibrations of large magnitudes, and so the operative stimulus in these instan-

ces may be considered as intermittent pressure variations of the surrounding medium evoking responses through the lateral line system. Although through behavioural experiments as reported here and by the previous authors, the direct response of the labyrintnectomised fishes to low frequency sounds could not be demonstrated, the notable difference in the intensity thresholds of the intact fishes and fishes with ear alone suggest that the lateral line organs have some definite part to play in the sound perceptive capacity of the whole fish. However, a knowledge of such a share of the lateral line organs could only be gained by further experiments on other fishes and also by an electrophysiological study of these sense organs.

(5) *Acknowledgments*

I wish to thank Dr. C. P. Gnanamuthu, M.A., D.Sc., F.Z.S., Director, University Zoology Research Laboratory, for outlining the problem and for his unfailing guidance during the course of this work. My thanks are also due to Dr. S. Krishnaswamy, M.Sc., Ph.D., Reader of this department for his useful discussions.

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Coulogravimetric Technique for the Estimation of Chloride and Thiocyanate Ions

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ABSTRACT

Coulogravimetry has been shown to be a reliable and accurate method for the estimation of thiocyanate and of chloride present in mixtures. The conditions necessary for obtaining the maximum accuracy of estimation have been worked out.

Introduction

Coulogravimetry introduced by MacNevin, Baker and McIver (1953) is a very recent electro-analytical technique which combines coulometry and electrogravimetry. By constant potential coulometry alone it is not possible to estimate separately mixtures of ions like chloride and bromide because of co-deposition. So MacNevin and co-workers suggested and developed the technique of coulo-gravimetry which involves the determination of (1) the increase in weight of a silver anode by the simultaneous deposition of both the halides (2) the number of coulombs required for the deposition by the ordinary coulometric method. From these two data the weights of chloride and of bromide present in the solution could be separately calculated. Subsequently MacNevin and McIver (1955) have adopted the method for the determination of zinc and cadmium occurring in a mixture by using a mercury cathode. Apparently no further work has been done on this subject.

The object of the present investigation has been to study the utility of this technique for the separate estimation of chloride and thiocyanate ions when present in a mixture. Coulometric analytical work previously done in this laboratory (Ibrahim, 1957) has shown that separate estimation of the chloride and the thiocyanate ions present in aqueous solutions is not practicable because of the error caused by co-deposition. For such a case coulo- gravimetry suggests itself as a possible method of estimation.

Experimental

Apparatus

For the present investigation the standard type of apparatus recommended by Lingane (1945, 1948, 1949) was found to be satisfactory.

Potential control

Manual control of potential was found to be quite satisfactory. The source of the direct current was a set of large capacity lead storage batteries and the constant potential was maintained by adjustment of a sensitive potential divider. The potential of the working electrode was measured in a potentiometric circuit against a saturated calomel electrode using an accurate Fisher potentiometer.

The Coulometer

The coulometer used was of the Lingane design (Lingane, 1945). It was accurately calibrated and found to have an efficiency of 99·9%. The electrolyte was 0·5 M potassium sulphate and the vapour pressures used for correcting the barometric pressure at different temperature are given below:

Temperature, °C.	25	26	27	28	29	30
Vapour pressure, mm. Hg.	23·3	24·7	26·2	27·8	29·4	31·2

MacNevin and co-workers (1953) have observed that the hydrogen-oxygen coulometer gives 1 to 2% low results sometimes and attributed the error to a certain mould developing in the electrolyte. The present authors also observed the formation of a mould and consequent low results arising from it. Use of freshly prepared potassium sulphate solution eliminates this difficulty.

The Cell

The cell used was a 250 ml. beaker, completely blackened to minimise the photolysis of silver salts. The solution was vigorously stirred using a magnetic stirrer. Suitable provision was made in the cell for bubbling an inert gas like hydrogen for expelling the dissolved oxygen.

The Electrode

All estimations described in this paper involve the formation of an insoluble silver salt at the anode. The anode was a silver electrode obtained by electro-deposition of silver on a cylindrical

platinum gauze electrode, the deposition being carried out from a cyanide bath (Brown, 1934) at 8 mA as described by Carmody (1929). An inner platinum gauze electrode served as cathode. A saturated calomel electrode was used as reference electrode. The circuit diagram for the estimation is given in Figure 1.

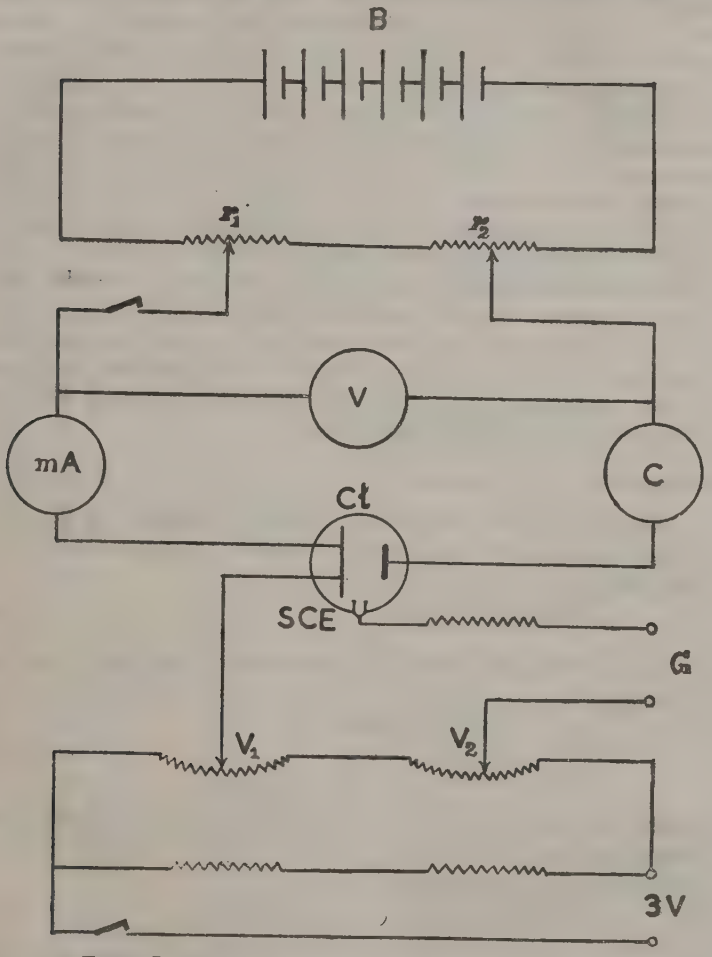

FIGURE I. CIRCUIT DIAGRAM OF THE EXPERIMENTAL SET-UP

B Battery; C Coulometer; Cl Cell; V Voltmeter (0-15 V); V_1 0-1·6 V; V_2 0-0·16 V; G Galvanometer; mA Milliammeter (0-200 mA); r_1 Rheostat (6 ohms); r_2 Rheostat (10 ohms); S.C.E. Saturated Calomel Electrode; 3V Potentiometer battery of 3 volts

Procedure

Potassium chloride and potassium thiocyanate of A. R. grade were used. Thiocyanate was standardised using Volhard's method. The silver anode and the platinum cathode, after thorough rinsing with water, were dried at 105°C to constant weight and weighed. The sample containing chloride and thiocyanate was pipetted into the cell and the supporting electrolyte (0·2 M sodium acetate and 0·2 M Acetic acid buffer having a pH of 5) was added until the volume totalled 140 ml. 10 ml. of 5% barium nitrate solution was also added. From the buffer solution the dissolved oxygen was expelled by bubbling hydrogen for about 15 minutes. The electrolysis was started at + 0·22 volts vs. S.C.E., but when the current fell around 15 to 20 mA., the potential was increased to + 0·25 volts vs. S.C.E. for the remainder of the electrolysis. The entire electrolysis required around 2 to 2½ hours and was considered complete when the current dropped to 1 to 1·5 mA. The residual current was however higher than is usual in coulometric analyses, but the reaction was found to be complete as shown by the spot tests. The electrodes were then washed, dried to constant weight at 105°C and weighed.

Calculation of the Results

The increase in weight $\triangle W$ of the silver anode is the sum of the weights Wcl and W_{CNS} of chloride and thiocyanate ion deposited.

$$\triangle W = Wcl + W_{CNS} \qquad .. \quad (1)$$

Representing the number of coulombs of electricity passed by Q, we have

$$\frac{Q}{96500} = \frac{Wcl}{35{\cdot}46} + \frac{W_{CNS}}{58{\cdot}11} \qquad .. \quad (2)$$

where 35·46 and 58·11 are the equivalent weights of chloride and thiocyanate ions respectively. Solving equations (1) and (2) Wcl and W_{CNS} can be evaluated.

$$Wcl = 9{\cdot}428 \times 10^{-4}\ Q - 1{\cdot}565\ \triangle W \qquad .. \quad (3)$$

A small concentration of silver ion formed in the solution at + 0·25 volts causes deposition of a small amount of silver on the platinum cathode because of the back-ground current (MacNevin *et al*, 1953). The total weight of silver thus deposited was

TABLE 1

Coulogravimetric Estimation of Chloride and Thiocyanate.
Supporting Electrolyte:—0·2 M NaAc—0·2 M HAc containing Barium nitrate.
Potential of the working electrode:—

Initial: +0·22 V vs. S.C.E.
Final: +0·25 V vs. S.C.E.

Ratio of Cl: CNS	Taken (mg.)		Found (mg.)		Absolute error in (mg.)		Relative error %	
	Cl	CNS	Cl	CNS	Cl	CNS	Cl	CNS
1:20 ..	2·98	60·10	2·93	60·31	−0·05	+0·21	1·70	0·35
1:10 ..	6·38	66·11	6·20	66·30	−0·18	+0·19	2·80	0·29
1:6 ..	15·91	90·15	15·89	89·88	−0·02	−0·27	0·13	0·30
1:4 ..	15·91	59·85	15·87	59·49	−0·04	−0·36	0·25	0·60
1:3 ..	15·91	48·08	15·89	47·89	−0·02	−0·19	0·13	0·40
1:2 ..	31·82	59·85	31·63	59·75	−0·19	−0·10	0·60	0·17
1:1 ..	31·82	29·93	31·77	29·80	−0·05	−0·13	0·16	0·43
2:1 ..	63·64	29·93	63·56	29·77	−0·08	−0·16	0·13	0·53
3:1 ..	95·67	29·93	95·52	29·74	−0·15	−0·19	0·16	0·63
6:1 ..	95·67	15·03	95·25	14·89	−0·42	−0·14	0·44	0·93
8:1 ..	95·67	12·02	95·12	11·82	−0·55	−0·20	0·57	1·66
15:1 ..	89·40	6·01	88·71	5·92	−0·69	−0·09	0·77	1·50

found to be of the order of 0·5 to 1·5 mgm. in the case of chloride-bromide mixtures by MacNevin *et al.* (1953). But due to the long duration of electrolysis in this case the amount of silver thus deposited ranged from 3 to 5 mgms. A correction of 0·89 coulombs for 1 mgm. of silver has to be made from the coulometer reading and this weight of silver must be added to $\triangle W$. These corrections are made in the results shown in Table I.

Results and Discussion

The data in Table I illustrate the accuracy of the method for the separate estimation of thiocyanate and of chloride when present together for widely different ratios of Cl : CNS ranging from 1 : 20 to 15 : 1. The magnitude of the error tends to increase for high Cl : CNS ratio, but is of a low order for lower ratios even when the thiocyanate ion is twenty times as much as chloride ion. It was also found that accurate results can be obtained only if the solution contains barium nitrate as supporting electrolyte besides the acetic acid-acetate buffer. In the absence of barium nitrate the results show wide variation on the positive and negative sides, presumably due to the formation of thiocyanogen.

However, one disadvantage of the method is that the estimation takes a comparatively long time for completion and the residual current was also found to be not less than 1·5 mA. This was not unexpected in view of the observation reported by Nair and Ibrahim (Nair and Ibrahim, 1956) in the estimation of thiocyanate in aqueous medium by constant potential coulometry at even higher potentials like + 0·38 volts vs S.C.E., the duration of electrolysis was found to be 90-100 minutes with a residual current of the order of 2 mA. Such a high potential cannot be employed for the estimation of chloride-thiocyanate mixtures, because at + 0·38 volts all the chloride will be co-deposited and then the metathetical reaction

$$AgCl + CNS^- = AgCNS + Cl^-$$

will take place spontaneously (Lingane, 1953). Hence the use of lower voltage for the estimation is justified, even though the duration of the estimation is somewhat prolonged. In spite of these drawbacks inherent in the method, the results shown in Table I indicate the usefulness of the method as an accurate analytical procedure for the estimation of chloride and of thiocyanate in mixtures of the two.

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Nutritional Mechanism of the Seed

1. *Nutritional mechanism of the embryo sac**

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In the Angiosperms the female gametophyte or the embryo sac is a highly reduced simple structure when compared with the Gymnosperms. The development of the embryo sac follows the Polygonum type in a majority of flowering plants. The most important structure, differentiated in the mature embryo sac is the egg. The egg cell is very important because after fertilisation it produces the embryo, which in turn is the forerunner of the future young plant. So, since the egg is developed in the embryo sac, a proper nutritive supply for it is very essential.

The highly reduced embryo sac develops within a nucellus which is either crassinucellate as in the Archichlamydeae or tenuinucellate as in the Sympetalae. In the less evolved families the embryo sac is surrounded by a nucellus which acts as a nutritive tissue; whereas in the more evolved families, particularly the Sympetalae, the scanty nucellus is completely crushed by the developing embryo sac. Therefore, there are various nutritive devices for the proper nutrition of the embryo sac in which the egg is organised.

When we compare the nucellus and female gametophyte of the Angiosperms with the Gymnosperms the situation is different. The nucellus in the Gymnosperms is a well developed massive tissue. The female gametophyte which develops and completely replaces it is a very elaborate, highly differentiated tissue broadly demarcated into an upper reproductive zone where the archegonia appear and a lower broad storage zone, consisting of cells densely packed with starch grains. The egg which develops in the archegonium can easily depend on the storage tissue of the female gametophyte for its nutrition. On the other hand the

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female gametophyte in the Angiosperms is a greatly reduced structure with no elaborate tissue differentiation as in the Gymnosperms; hence, special nutritive devices are seen in Angiosperms and these are extremely varied and most interesting.

In the nutritional mechanism of the embryo sac the tissues around the embryo sac (or sporophytic tissues) and the embryo sac and its constituent parts (or gametophytic structures) are also involved. Among the sporophytic tissues which play an important part in this nutritional mechanism we may first start with the placenta to which the ovule is attached by the funiculus. The placenta is a highly vascularised tissue, densely charged with nutritive materials. In the Lentibulariaceae, there is a massive free central placenta. During the growth of the ovule, in *Utricularia coerulea* (Kausik, 1938) and *U. flexuosa* (Khan, 1954), there differentiates a group of placental cells near the base of the ovule and close to the funiculus, to constitute the placental nutritive tissue. The cells have dense protoplasmic contents and are organised into a compact ovoid mass which forms a distinctive feature of the placenta whether in transverse or in longitudinal section. In older stages each mass is surrounded by a sheath of two or three layers of cells. The vascular supply of the placenta, in longitudinal section, appears in the form of a "tree". Near the base of the placenta the vascular strands form a column comparable to the trunk of a tree. At higher levels the strands undergo branching. The ultimate ramifications approach the group of nutritive cells in the peripheral region. Thus, the nutritive cells do not form isolated islands but are in communication with the vascular supply of the placenta. The upper bulbous portion of the embryo sac protrudes beyond the ovule into the ovarian cavity and its apex is burried in the placental nutritive tissue. Thus, the extra ovular embryo sac is supplied with food material by this specially organised nutritive tissue of the placenta.

The nucellus in which the embryo sac develops acts as a very important nutritive tissue. In the primitive families of Angiosperms it is very massive. It consists of a homogeneous mass of parenchymatous cells with dense protopasmic contents and sometimes reserve food materials of the nature of starch grains. The membrane of the embryo sac draws nutrition from the surrounding nucellar tissue by surface absorption.

In certain Angiosperms, two specialised tissues of nucellar origin which are regarded as connected with the nutritional

mechanism of the embryo sac are the Hypostase and Epistase respectively.

Just at the level of the origin of the two integuments and directly below the embryo sac, there is often a well-defined but irregularly outlined group of nucellar cells which are usually poor in cytoplasmic contents but have partially lignified or suberized walls composed of a highly refractive material. The name hypostase was assigned to this patch of cells by Van Tieghem (1901) and he regarded that it formed a sort of barrier or boundary for the growing embryo sac and prevented it from pushing it into the base of the ovule. Because of the peculiar position of this tissue directly above the termination of the vascular supply of the ovule, Goebel (1933) suggested that it is indicative of its relation to the water economy of the embryo sac. Johansen (1928) has observed such a hypostase in members of Onagraceae and he regards that this tissue stabilises the water balance of the resting seed over the long period of dormancy during the hot, dry season. While the function of the hypostase is still in doubt, morphologically it is a very characteristic feature of certain families like Melastomaceae (Subramanyam 1942, 1944, 1946, 1948, 1953) and Onagraceae (Johansen, 1928; Subramanyam and Govindu, 1948) and certain other genera; *Zostera* (Dahlgren, 1939b), in particular, offers an especially good instance of a well-developed hypostase. The hypostase may not always consist of thick-walled cells. It can be thin-walled as in *Knautia* (Lavialle, 1925) and *Dionaea* (Smith, 1929). The cells of the hypostase in *Allium odorum* (Haberlandt, 1923) become richly cytoplasmic and appear similar to the epithem of many hydathodes. Haberlandt (l.c.) considers it to be a sort of glandular tissue secreting some hormone or enzyme required for the growth of the embryo sac.

Van Tieghem (l.c.) also reported the occasional presence of a similar well-marked tissue in the micropylar part of the ovule which he called the epistase. Usually it originates from the apical cells of the nucellar epidermis which show a marked radial elongation and become somewhat thickened or suberized. An epistase is organised in *Castalia* (Cook, 1906) where the epidermal cells lying at the apex of the embryo sac show a very pronounced sclerification; in *Costus* (Boehm, 1931), the inner tangential walls of these cells become conspicuously thickened. In *Fouquieria* (Khan, 1943) where the nucellus is scanty, the cells of the inner integument near the micropylar region of the ovule differentiate into an epistase.

The integumentary tapetum is an important tissue concerned with the mechanism of nutrition of the embryo sac. In those plants in which the nucellus is soon disorganised, as in most members of Sympetalae, the embryo sac comes in direct contact with inner layer of the seed coat. The cells of this layer frequently become specially differentiated from the rest by their form and contents. They show a pronounced radial elongation and sometimes become binucleate. They also contain plenty of starch grains. Since they show similarities with the cells of the anther tapetum, this layer is known as the integumentary tapetum or endothelium. In *Stylidium graminifolium* (Subramanyam, 1951) the integumentary tapetum is especially conspicuous and consists of narrow transversely elongated cells with large nuclei and dense cytoplasm. It is interesting to find that in a family like Scrophulariaceae (Krishna Iyengar, 1942) as a whole there are various grades in the development of the integumentary tapetum. In *Sopubia* the endothelium consists of a single layer of cells of uniform size. The next condition is seen in *Tetranema* and *Torenia* where the chalazal and micropylar ends of the tapetal sheath are generally composed of smaller cells, while the larger cells are confined to the middle of the sheath. In *Verbascum* the larger and smaller cells regularly alternate, the smaller cells being single as in *V. thapsus* or in pairs as in *V. montanum* (Schmid, 1906). In *Celsia* this regularity is wanting. The intercalation of smaller cells may or may not be found and when these are present they may be either solitary or in pairs. Finally, in *Centranthera* the largest cells of the row are towards the chalazal end, in the neighbourhood of the chalazal endosperm haustorium, which is here the least efficient as a haustorium.

In *Lobelia trigona* (Kausik, 1935) the tapetal cells at the chalazal end of the embryo sac have denser contents than those situated at a higher level. Apparently they absorb food from the cells of the chalazal nutritive tissue and transport it to the embryo sac. However, when the embryo sac is mature, the tapetal cells become thick-walled and impervious, so that this layer has two separate functions during the maturation of the seed, at first nutritive and then protective.

There seems to be no doubt that the endothelium is a nutritive layer whose chief function is to serve as an intermediary for the transport of food materials from the integument to the embryo sac. Some workers also claim that it contains diastase and other enzymes

which convert the food into a soluble form for the use of the embryo sac. In later stages, when the embryo is approaching maturity, the inner surface of the endothelium becomes cutinised and this layer seems to take up a protective instead of nutritive function. Thus, the tapetum fulfils the functions of digestion, absorption, storage and protection.

A tapetum of nucellar origin is reported in certain members of Lythraceae. In *Lawsonia inermis* (Joshi and Venkateswarlu, 1935) and *Ammannia baccifera* (Joshi and Venkateswarlu, 1936) the cells surrounding the megaspore mother cell are slightly richer in cytoplasm and stain somewhat deeper than the cells of the nucellus and thus form a faintly differentiated tapetum. This is crushed afterwards by the growth of the embryo sac.

The vascular supply of the ovule is another important device for the transport of water, mineral salts and other food materials for the developing embryo sac. Generally the vascular bundle entering the ovule through the funiculus terminates at the chalaza but in some plants it gives out branches, a few of which enter the integument. If two integuments are present the branches enter only the outer integument or both the outer and inner integuments. Such integumentary vascular bundles are now known to occur in a number of families, both primitive and specialised.

The occurrence of vascular elements in the nucellus is much rarer. Benson (1894), Frye (1902) and Benson, Sandy and Berridge (1906) identified some nucellar tracheids in *Castanea, Asclepias* and *Carpinus* respectively, but they showed no connection with the vascular bundle of the ovule. Orr (1921) has reported the occurrence of connecting nucellar tracheids in a few members of the Capparidaceae and Resedaceae. A feature of unusual interest in the ovule of *Exocarpus cupressiformis* (Ram, 1959a) is the presence of tracheidal cells which differentiate at the megaspore mother cell stage and show spiral thickenings. During the development of the female gametophyte a row of tracheidal cells connect the basal end of the embryo sac with the vasculature of the ovary. Among recent records, in *Agave* (Grove, 1941) and *Strombosia* (Fagerlind, 1947) the vascular strand of the ovule is said to penetrate into the nucellus upto the base of the embryo sac and in *Magnolia* (Earle, 1938) it gives out short branches in the chalaza, one of which is directed towards the embryo sac. In *Acalypha* (Landes, 1946) the main bundle of the ovule proceeds upto the hypostase and forms a number of short branches whose

ultimate ramifications extend into the nucellus upto a distance about one fifth of the length of the ovule. A very striking and interesting condition is reported by Swamy (1948) in *Casuarina,* where the funicular strand extends upto the base of the sporogenous tissue, some of whose cells elongate and themselves assume a conducting function instead of giving rise to embryo sacs.

At the chalazal region of the ovule where the funicular vascular strand terminates, the nucellar cells in this region differentiate themselves in various ways to serve a conducting and nutritive role. In certain taxa of Lythraceae (Joshi and Venkateswarlu, 1935, 1936) below the megaspore cell differentiates a row of two or three cells which are much richer in cytoplasm than the other nucellar cells. The cells of this axial row undergo repeated divisions and give rise to a strand of slightly thick-walled, elongated cells rich in cytoplasm. This has most probably a conducting function connecting the vascular supply of the ovule ending in the chalaza with the antipodal end of the embryo sac. The presence of such a chalazal conducting strand is reported in certain members of other families like Campanulaceae (Kausik and Subramanyam, 1947) and Liliaceae (Subramanyam and Nagaraja Rao, 1952). In *Lobelia cardinalis* (Cooper, 1942) a number of thin-walled elongated cells with dense cytoplasm and ovoid nuclei extend from the tip of the vascular strand towards the chalazal end of the embryo sac. Only few parenchymatous cells intervene between these cells and the nutritive tissue of the chalaza. According to Cooper (1942) these parenchymatous cells remain vacuolate until the ovule is fairly mature and probably function in the osmotic conduction of water and food material from the conducting strand to the developing seed. In other members of Lobeliaceae (Kausik 1935, 1938; Subramanyam 1949, 1953), just below the antipodal end of the embryo sac, a chalazal nutritive tissue made up of cells with dense cytoplasm and prominent nucleus is organised. It acts as a feeding tissue and part of it is used up before fertilisation and the rest soon after the formation of the chalazal haustorium.

We may now turn to the nutritive devices seen in the embryo sac and its constituent parts. Cyologically it represents the highly reduced female gametophytic tissue. The elongated cylindrical nature of the embryo sac is itself a very suitable device in its nutritional mechanism; further, in the majority of angiosperms the entire surface of the embryo sac serves an absorptive function,

demolishing the adjacent cells of the nucellus and even the inner layer of the integument.

In some plants, however, more active growth is seen at the ends of the sac. In *Phaseolus* (Weinstein, 1926) and *Melilotus* (Cooper, 1933) the embryo sac ruptures the nucellar epidermis and grows beyond it, so that more than one third of it lies in contact with the cells lining the micropylar canal. In *Arechavaletaia* (Ventura, 1937) and *Kirengeshoma* (Mauritzon, 1939) it protrudes out of the endostome and comes to lie in the exostome. In *Philadelphus* (Mauritzon, 1933), *Thesium* (Schulle, 1933), *Galium* (Fagerlind, 1937), *Utricularia* (Kausik, 1938; Khan, 1954) and certain members of the Scrophulariaceae like *Vandellia* and *Torenia* (Krishna Iyengar 1940, 1941) the nucellus breaks down completely at a rather early stage and the naked embryo sac protrudes out of the ovule, establishing direct contact with the placenta and digesting its way into the tissue of the latter. Strangest of all are some genera of the Loranthaceae in which ovules and integuments are absent in the usual sense and the embryo sacs undergo a remarkable elongation towards both the top and the bottom. At the lower end they are soon stopped by a pad of collenchymatous cells, but the upper part continues to grow, sometimes reaching a considerable distance into the style. Fertilisation occurs here by the incoming pollen tubes and the embryos are thrust down again by the elongating suspensors.

The upward elongation of the embryo sac in various members of the subtribe Loranthoideae of Loranthaceae reaches various heights of the style (Maheshwari, Johri and Dixit, 1957). In *Macrosolen cochinchinensis* the tips of the embryo sacs extend only to the base of the style; upto one fifth the length of the style in *Lepeostegeres gemmiflorus;* half the style in *Helicanthes elastica* and *Lysiana exocarpi;* and to two thirds the height of the style in *Taxillus sclerophyllus.* In *Helixanthera hookeriana* the apex of the embryo sac reaches upto the stigma and in *H. ligustrina* it grows as far as the stigmatic surface and lies below the papillate layer of the stigma.

In other plants it is a downward growth which is more striking. In members of Lobeliaceae (Kausik, 1935; Subramanyam, 1949) and Stylidiaceae (Subramanyam 1950, 1951) the behaviour of the chalazal end of the embryo sac deserves mention. In these families (Subramanyam, 1953) it forms a process which grows

beyond the antipodals and projects into the chalazal nutritive tissue forming a weak haustorium which is later replaced by the more aggressive endosperm haustoria. Barnes (1885) has observed that in *Campanula americana* the antipodal end of the embryo sac enlarges more or less abruptly forming a bulbous chalazal embryo sac haustorium. In several members of the Centrospermales (Oksijuk, 1927; Artschwager and Starrett, 1933; Joshi, 1936; Cooper, 1949), Loranthaceae (Narayana, 1958 a, b; Dixit, 1958) and Santalaceae (Ram, 1959a, b) the embryo sac pushes forward at the chalazal end and digests its way through the nucellus while the antipodals remain *in situ* and are left behind in a lateral position. This "caecum" seems to be a very effective haustorial organ. Cases are also known where the embryo sac haustorium arises laterally rather than from the pole of the embryo sac. Before fertilisation a lateral caecum arises from the embryo sac in *Commandra umbellata* (Ram, 1957) on the funicular side, just below the level of the egg apparatus. It grows through the ovule and enters into the spirally twisted column and extends along the vascular strand. In *Nuystia floribunda* (Narayana, 1958b) a remarkable feature of the embryo sac is the development of a lateral caecum or haustorium near the upper end which is sometimes branched. It arises as a small, blunt, lateral protruberance at about the level of the egg apparatus and elongates into the stylar canal and sometimes penetrates even in the stylar tissue. The embryo sac of *Exocarpus strictus* (Ram, 1959a), a member of the Santalaceae, is rather extremely interesting because numerous finger-like outgrowths arise from the middle of the embryo sac and hang over the lower portion like a skirt. Though their exact role is not definitely known, it is probable they provide an additional absorptive surface.

The food reserves in the embryo sacs are the starch grains and they also play an important part in the nutrition of the embryo sac. Though it is considered that the angiosperm embryo sac is devoid of any appreciable food reserves, there are now several records of the occurrence of starch in embryo sacs. In certain families like Aizoaceae, Cactaceae, Portulacaceae, Bruniaceae, Tiliaceae, Crassulaceae and Asclepiadaceae, the occurrence of starch grains in the mature embryo sac is a very common phenomenon. Dahlgren (1927, 1939a) has reviewed this subject very well (see also Maheshwari, 1950). The stage at which the starch makes its appearance in the embryo sac varies in different plants. In *Loranthus pentandrus*, Treub (1883) saw starch grains

even at the megaspore mother cell stage; in *Psychotria* (Fagerlind, 1937) starch appears at the dyad cell stage; in *Sedum* (D'Hubert, 1896) at the functioning megaspore stage; in *Portulaca oleracea* (Cooper, 1940) at the binucleate stage; and in *Corchorus triloc*ularis (Stenar, 1925) at the four nucleate stage. In the majority of plants, however, the starch appears when the embryo sac is mature and reaches a maximum shortly after fertilization, gradually decreasing in postfertilization stages.

A few cases are on record in which the starch occurs not merely in the cavity of the embryo sac but also in the cells of the egg apparatus and rarely even in the antipodal cells. Occurrence of starch grains in egg are seen in *Acacia baileyana* (Newmann, 1934), *Korthalsella opuntia* (Rutishauser, 1937), *Portulaca oleracea* (Cooper, 1940), *Phryma leptostachya* (Cooper, 1941) and *Sedum ternatum* (Subramanyam, 1955). In *Korthalsella* (Rutishauser, 1937) starch grains are found in antipodal cells and in *Sedum ternatum* (Subramanyam, 1955) they occur in synergids.

Certain oily bodies of unknown nature persist from the megaspore mother cell stage to the formation of the mature embryo sac in *Sonneratia* (Venkateswarlu, 1937; Mauritzon, 1939) and in *Aspidistra* (Golaszewska, 1934) large raphides have been seen in the mature embryo sacs. The significance of these structures in the economy of the embryo sac is not known so far.

The synergids, though they are ephemeral and disappear soon after fertilisation, sometimes enlarge, persist and behave as haustoria, thus helping in the nutrition of the embryo sac. In some cases, however, one or both of them may persist for a time and show signs of considerable activity. In *Allium unifolium* and *A. rotundum* (Weber, 1929) this behaviour is particularly pronounced and one of the synergids begins to degenerate only after the development of the embryo is well under way. *Nothoscordum* (Stenar, 1932), *Limnanthes* (Fagerlind, 1939) and *Albuca* (Eunus, 1950) are essentially similar; and in some Cucurbitaceae (Kirkwood, 1905) both the synergids become large and prominent and seem to play an important role in the nutrition of the embryo sac. The extension of the synergids beyond the limits of the embryo sac is seen in Compositae. Dahlgren (1924) found that in *Ursinea* and *Calendula* the synergids elongate so much that their tips project to a considerable distance into the micropyle and outside it, sometimes reaching as far as the funiculus.

The antipodals are usually short-lived. Frequently they increase in size or number. When they increase in size they behave as aggressive haustoria absorbing nutrition from surrounding tissue. An increase in the number of cells is noticed in some members of Gentianaceae (Stolt, 1921), where the three antipodal cells divide to form ten to twelve cells. In the Gramineae a still larger number of cells is produced. In *Sasa paniculata* (Yamaura, 1933), a member of Bambusae, as many as three hundred antipodals have been reported.

In several taxa of Rubiaceae like, *Putoria* (Fagerlind, 1936a), *Galium* (Fagerlind, 1937) and *Rubia* (Fagerlind, 1937; Vekateswarlu and Rajeswara Rao, 1958) the basal antipodal cell is often elongated and acts as an aggressive haustorium. In *Phyllis* (Fagerlind, 1936b) all the three antipodals are swollen, the basal becomes eight nucleate and each of the upper two four nucleate and these behave as antipodal haustoria. An increase in the number of antipodal cells and the number of nuclei per antipodal cell is well known in the Compositae. In *Grindelia squarrosa* (Howe, 1926) only two antipodal cells are formed, the one nearer the micropyle being binucleate. One or both of these cells undergo further development, growing laterally into the integument for a considerable distance. In *Artemisia* (Diettert, 1938) the number of antipodal cells varies from three to six and each cell may have two or more nuclei. The basal antipodal cell frequently elongates and penetrates through the chalazal tissue, finally entering the ovarian chamber. The antipodal cells of some members of the Ranunculaceae (Osterwalder, 1898) become greatly enlarged and assume a glandular appearance. The antipodal cells with their pointed lower ends in the Campanulaceae, Lobeliaceae and Stylidiaceae (Subramanyam, 1953) seem to be adapted for the absorption and conduction of food to the upper part of the embryo sac.

In some plants the nucellar nuclei migrate into the embryo sac. As the embryo sac grows and enlarges the adjacent cells of the nucellus become flattened and crushed. Their walls, which are very thin and delicate, get ruptured and the contents—both cytoplasm and nuclei, or only the latter—may "wander" into the embryo sac and become incorporated in it. The nuclei of the nucellar cells in *Hedychium gardnerianum* (Madge, 1934), lying below the hypostase, migrate "from cell to cell" through the small holes in the walls until they reach the hypostase. Here their progress is stopped for a time and groups of twenty or thirty

nuclei collect together, surrounded by the rugged cell walls of the ruptured cells. Some of the nuclei now make their way around the hypostase into the cavity of the embryo sac, where they are believed to serve a nutritive function. In *Pandanus* (Fagerlind, 1940) which has no thick-walled hypostase, the nucellar cells lying beneath and on the sides of the young embryo sac show a marked tendency to enlarge. Their nuclei become swollen and the plasma assumes an appearance similar to that of the embryo sac. The enlarged nuclei soon approach the embryo sac wall, which becomes perforated at such points. Gradually the pores become wider and finally the entire separating wall is absorbed. The embryo sac now encroaches upon these areas and soon incorporates them, coming in contact with newer cells which may also meet the same fate. Even at the four nucleate stage, as many as ten or more nucellar cells become included inside the embryo sac in this fashion. Thus, in the mature embryo sac, the egg apparatus and antipodals contain haploid nuclei and others are diploid.

There are some cases where haustoria are developed from megaspores at the linear tetrad stage and they help in the nutrition of the embryo sac. These peculiar instances are seen in *Rosularia, Sedum* (Mauritzon, 1933; Subramanyam, 1955), *Laurus* (Bambacioni-Mezzetti, 1935), *Potentilla* (Rutishauser, 1945) and some members of the Rubiaceae (Fagerlind, 1937). In these taxa, the megaspores give out lateral tubes, which subsequently grow upward and are in a competition with one another. In *Putoria* and *Galium* the tubes enter the integument. In *Sedum chrysanthum* (Syn. *Rosularia pallida*) bundles of megaspore tetrads are formed and every megaspore gives rise to a tube or haustorium; these grow into the upper part of the nucellus which now shows quite a tangle of haustorial processes competing with one another.

It is thus seen, that the nutritive devices noticed in the ovule, for the proper nutrition of the egg in the embryo sac, are extremely varied and most interesting. Both the sporophytic tissues around the embryo sac and gametophytic structures of the embryo sac are involved in this nutritional mechanism.

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Nutritional Mechanism of the Seed

2. *Nutritional mechanism of the embryo**

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After the pollen tube has discharged its contents into the embryo sac, one male gamete fuses with the egg (syngamy) and the other with two polar nuclei (triple fusion). This is the process of double fertilization which is a characteristic feature of Angiosperms. As a result of syngamy the zygote by further development produces the embryo which in turn constitutes the most important structure of the seed. Naturally, for a proper development of the embryo in the seed, its nutritional requirements should be adequately satisfied.

An important nutritive tissue that immediately surrounds the embryo is the endosperm. In the albuminous seeds, the endosperm forms a permanent storage tissue in the mature seed and persists until the germination of the seed. In the exalbuminous seeds, however, the endosperm is made use by the developing embryo and is no longer seen in the mature seed. In addition to the endosperm, in certain taxa, the nucellus persists in the developing seed, stored with plenty of food material when it is called the perisperm. The endosperm and perisperm are thus two important tissues concerned with the nutritional mechanism of the embryo. Further, the growing embryo also develops the special nutritive devices for absorbing nutrition from the surrounding tissues.

The endosperm is essentially a nutritive tissue because it functions as the main source of food for the developing embryo. In Gymnosperms it is haploid and forms a continuation of the female gametophyte. In Angiosperms, on the other hand, it is a new structure formed in most cases as a result of a fusion of the polar nuclei and one of the male gametes. Since all three of the fusing nuclei are usually haploid, the endosperm contains the

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triploid number of chromosomes. Endosperm formation is suppressed in three families, Orchidaceae, Podostemaceae and Trapaceae. Correspondingly the embryos in these families, since they have to develop in the absence of a nutritive tissue, form curious haustorial structures for drawing nutrition from the seed coat.

The endosperm serves as a physiological tissue and supplies the necessary amount of food material for the proper development of the embryo in the seed. The endosperm cells are usually isodiametric and store large quntities of food materials of the nature of starches and oils. It is present in the albuminous seeds in the form of a solid mass of tissue; in some taxa like *Cocos nucifera,* while the peripheral portion is cellular forming a compact tissue, the central portion remains hollow containing free endosperm nuclei floating in a fluid commonly called the "Coconut milk". The exact nature and proportions of food materials stored in the endosperm tissue vary from one plant to another. As a rule the walls are thin and devoid of pits, but when hemicellulose is the chief food reserve they are greatly thickened and pitted. In such cases they may be more or less homogeneous as in *Phytelephas,* or show a distinct stratification as in *Fritillaria.*

In grasses and some other plants, the peripheral layer of the endosperm functions like a cambium and produces on its inside a series of thin-walled cells which become packed with starch. As the seed approaches maturity, the outermost layer ceases to divide, its cells become filled with aleurone grains, and the walls become slightly thickened. There are two or three layers of aleurone cells in a taxon like *Oryza* (Juliano and Aldama, 1937). There is much uncertainty regarding the possible function of this aleurone layer. According to Haberlandt (1914) its chief function is not that of storage but the secretion of diastase and other enzymes so that the food materials stored in the endosperm may be available to the developing embryo in a soluble form.

Broadly there are three modes of endosperm formation. In the Nuclear type, the first division and several of the following ones are not accompanied by cytokinesis. The nuclei may remain free or become separated by walls during later stages. In the Cellular type, the first and most of the subsequent divisions are accompanied by wall formation. The third or Helobial type is intermediate between the Nuclear and the Cellular types. Here the first division is followed by a transverse wall, resulting in a micropylar and chalazal chamber. Subsequent divisions are free

nuclear and may take place in both chambers, but as a rule the main endosperm tissue is formed by the micropylar chamber only.

An interesting feature of the endosperm is its capacity to develop haustoria which, in turn, penetrate into the tissues at the micropylar and chalazal regions of the ovule, absorb nutritive materials and transfer the same for the developing embryo. The endosperm haustoria, in their development, growth and behaviour are extremely varied. The haustorial behaviour of the endosperm can be illustrated by some examples.

The haustorial structures met with in some members of Proteaceae (Kausik, 1938a, b, 1942) requires a special mention. Here most of the endosperm nuclei are distributed in the upper portion of the embryo sac. Cell wall formation is restricted to this region, while the lower portion of the sac remains free nuclear. In *Macadamia ternifolia* this part forms several prominent lobes or diverticulae which invade the nutritive tissue at the chalazal end of the ovule and function as haustoria. At later stages, when the food material in the chalazal cells is completely used up, the activity of these haustorial lobes comes to an end. In another taxon of Proteaceae, *Grevillea robusta* the lower coenocytic part of the endosperm grows in the form of a coiled and tubular worm-like structure, which has been aptly designed as the "vermiform appendage". It serves as a haustorium of a very aggressive type whose coils invade the cells of the chalaza and bring about their virtual dissolution. Later the appendage becomes partioned into several large chambers which undergo further subdivisions into smaller units, so that the cells formed in this way constitute a kind of secondary endosperm tissue.

A haustorial activity of the chalazal part of the endosperm which gradually digests the persistent nucellar base or even encroach on the chalazal tissue is seen in several taxa of Leguminosae (Anantaswamy Rau, 1955). In *Glycine javanica* (Anantaswamy Rau, 1951a) the short haustorial process digests the basal part of the nucellus and in later stages gets separated into multinucleate bits, though no walls are laid. *Stylosanthes*, a member of the tribe Hedyserae, shows a peculiar organisation of the endosperm. Cell formation is absent and the endosperm nuclei which lie in dense cytoplasm, close to the border of the embryo sac, become hypertrophied and may present nuclear fusions (Anantaswamy Rau, 1952). The cytoplasm penetrates into the integumental layer in between

the cells, bringing about the separation of these integumental cells. After fertilization the ovule in *Rothia trifoliata* (Anantaswamy Rau, 1951b) shows the development of a large multinucleate endosperm which extends by a haustorium at the expense of the cells in the base of the ovule. This lateral haustorium is organised on the funicular side of the developing seed and in this diverticulum are seen the enlarged endosperm nuclei and dense cytoplasm.

A very well developed and aggressive micropylar haustorium occurs in *Impatiens* (Dahlgren, 1934). The first division of the primary endosperm nucleus gives rise to two chambers. The micropylar chamber, which is the smaller, divides transversely into three cells. The uppermost of these, containing the zygote, forms a giant haustorium whose branching arms extend as far as the funiculus.

An aggressive chalazal endosperm haustorium is developed in *Exocarpus sparteus* (Ram, 1959). The primary endosperm nucleus divides much earlier than the zygote. The first division is followed by a transverse wall partitioning the embryo sac into two chambers. The micropylar chamber divides transversely while the chalazal undergoes a longitudinal division. The two lower cells do not divide any further but elongate enormously, penetrating into the base of the ovary and functioining as haustoria. During elongation, they become separated from each other, grow independently and develop numerous finger-like processes at the basal end, thus acting as a very efficient chalazal endosperm haustorium.

In *Nothapodytes foetida,* Swamy and Ganapathy (1957) have described a new type of endosperm haustorium. In this plant the ultimate endosperm cell towards the chalazal end is concerned with the origin and development of the haustorium. The cell increases in size and puts forth a short caecum towards the chalaza. The quantity of cytoplasm increases rapidly and the nucleus begins to lose its spherical contour, so much so that in later stages it comes to assume unusually fantastic shapes associated with profound modifications of the intra-nuclear structures. The method of spread of the hausorium is most remarkable. The cytoplasm of the haustorium initial cell comes in contact with the adjacent cells of the chalazal tissue of the ovule and at the point of contact the cell wall becomes dissolved to form an aperture. The protoplasts of the haustorial and affected cells unite with one another. The nuclei of these cells become included in the haustorial cytoplasm, where they are soon absorbed.

The occurrence of endosperm haustoria, both micropylar and chalazal is a universal feature of the Scrophulariaceae. They show great variation in their number, structure, organisation and behaviour. Two instances of haustorial behaviour are worthy of mention. In *Rhamphicarpa longiflora* (Krishna Iyengar, 1942) the endosperm is *ab initio* cellular and the chalazal endosperm haustorium is the first to be organised and is a single binucleate organ. This begins to elongate into a tubular body and eats its way into the vascular traces of the integument. The terminal part is slightly bent and enlarged with two nuclei migrating into it. The cells in its neighbourhood show all stages of disintegration, demonstrating the aggressive nature of the haustorium. The two micropylar cells become binucleate and fuse at a very early stage by the dissolution of their separating wall. This haustorial body is tetra-nucleate and grows towards the chalaza, along the vascular traces of the hilum, digesting and disorganising the tissue coming against it and finally finding its way into the bend formed by the chalazal haustorium and enlarges distally. The micropylar haustorium is thus a highly aggressive tubular body. One or two nuclei are seen in this tube. At times the two haustoria (micropylar and chalazal) are so close and disorganisation so thorough that they almost communicate with each other—a remarkable feature of this plant. In *Centranthera hispida* (Krishna Iyengar, 1942) neither the micropylar nor the chalazal haustorium is very active, but there are formed instead some secondary haustoria. Some of the endosperm cells just beneath the micropylar haustorium become active at a very early stage and develop lateral haustorial tubes which eat their way into the endothelium and begin to digest the integumentary tissue. These tubes are simple, unbranched, uninucleate and highly aggressive, ending just below the epidermis. The growth is lateral and then towards the chalaza; at times the ends of these haustoria coalesce.

In members of Campanulaceae, Lobeliaceae and Stylidiaceae (Subramanyam 1949, 1951, 1953) both the micropylar and chalazal haustoria are aggressive structures, although the micropylar persists for a longer period than the chalazal. In *Levenhookia dubia* (Subramanyam, 1950) and *Stylidium graminifolium* (Subramanyam, 1951) the behaviour of these haustoria is especially interesting. When the micropylar haustorium is well developed, lateral processes are formed from each of its cells and these begin to gradually descend down and grow in between the parenchymatous cells of the integument. The chalazal haustorium which is made

up of two uninucleate cells soon reaches the base of the seed, disorganising almost all the cells at the chalazal region of the ovule. Soon, the chalazal haustorium also behaves in an aggressive manner like the micropylar. Both the cells of the chalazal haustorium develop long tubular projections as in *Levenhookia dubia* (l.c.) or a number of processes as in *Stylidium graminifolium* (l.c.) and these in turn grow in between the cells of the integument. The endosperm tissue itself which lies between the two haustoria is made up of cells densely packed with starch grains except in the region immediately around the developing embryo. Probably the latter secretes an enzyme which dissolves the starch.

More remarkable still are the lateral haustoria reported in members of Pontederiaceae (Ono, 1928; Juliano, 1931; Banerji and Halder, 1942). The early stages of endosperm development are according to the Helobial type. The chalazal chamber remains small and has only about half a dozen nuclei or less. But the micropylar chamber shows active nuclear divisions and soon gives rise to two tubular outgrowths (one on each side of the chalazal chamber) which grow downward and invade the tissues of the chalaza. Subsequently, the main body of the chamber also elongates and fuses with the two haustoria to form a continuous mass of endosperm cells with the chalazal chamber still recognizable at the base.

In certain families of Angiosperms like Piperaceae, Amaranthaceae, Porulacaceae, Capparidaceae, Zingiberaceae and Cannaceae the nucellar tissue surrounding the embryo sac persists, becomes densely packed with food materials and this is now called the Perisperm. In this case the endosperm functions as an intermediary between the perisperm and the embryo, obtaining the food stored in the former and passing it on to the latter. In Amaranthaceae (Kajale, 1940) a good deal of nucellus is left in the centre of the mature seed and this represents the perisperm. The cells in it are densely filled with starch grains which serve as the reserve food for the embryo. The perisperm in *Celosia argentea* and *Amaranthus viridis* is a pearshaped body enclosed within the embryo. In *Allmania nodiflora* and *Pupalia lappacea* it becomes two-lobed due to the excessive growth of the cotyledons.

In *Cynastrum* (Fries, 1919; Nietsch, 1941) the nucellus and endosperm disappear during the development of the seed, but the cells in the chalazal part of the ovule, just above the vascular bundle, divide actively and form a very prominent tissue which,

alhough loose and possessed of many air spaces, soon becomes filled with fat and starch and serves as a substitute for the endosperm. Fries calls this tissue "chalazosperm".

The suspensor is a very important structure which plays a significant role in the nutritional mechanism of the embryo. It pushes the embryo deep into the endosperm, where it is surrounded by cells containing abundant food materials. In several plants the suspensor cells show a pronounced increase in size or give rise to prominent haustorial structures which penetrate between the cells of the endosperm and encroach upon the surrounding tissues of the ovule.

In some species of *Crotalaria* (Anantaswamy Rau, 1950) the massive multicellular suspensor shows a differentiation into an upper and lower part. The peripheral cells of the lower part project out and act as haustorial structures for the absorption of nutrition from the surrounding endosperm. In *Crotalaria retusa* and *C. striata* these tubular cells in the middle portion of the suspensor encroach on the neighbouring endosperm, nucellus and even integumental layers and absorb substances. The cells of the suspensor possess chloroplasts so that this organ also has a photosynthetic function in addition to its haustorial activity.

The suspensor haustoria of the Rubiaceae have been well known since the days of Hofmeister (1858) and later Lloyd (1902), Souèges (1925), Fagerlind (1937) and Venkateswarlu and Rajeswara Rao (1958) have given further details of their origin and structure. At first the suspensor is merely a filament of cells; later it becomes multicellular and the micropylar cells send out lateral protrusions which penetrate into the endosperm and swell at their distal ends. These cells are vesicular, contain abundant starch grains and have prominent vacuoles. The cytoplasm in these cells is mostly confined to the periphery; these cells thus form an effective intra-endospermal haustorium.

The suspensor haustoria of the Haloragaceae bear a remarkable resemblance to synergids. Stolt (1928) and Souèges (1940) have shown that in *Myriophyllum* the two-celled proembryo consists of a large basal cell and a much smaller terminal cell. The former divides longitudinally to form two daughter cells, which enlarge to such an extent as to occupy the entire space in the micropylar part of the embryo sac. They can be distinguished even at the time of differentiation of the cotyledons. In

Hypecoum (Souèges, 1943a, b), a member of Fumariaceae, the basal cell of the two-celled embryo does not divide but becomes greatly swollen and vesicular. The terminal cell divides diagonally into two unequal cells of which the larger cell becomes swollen like the basal cell. These two haustorial cells persist for a long time and appear like synergids.

Walker (1947) has given a detailed account of the origin of the massive haustoria of *Tropaeolum majus*. Here the basal cells of the proembryo divide more actively than the other cells. Such of the cells of this mass that lie on the side away from the funiculus give rise to a long haustorial process which pierces the micropylar part of the integument and finally enters the pericarp. Slightly later, a second protuberance arises from those cells of the mass which lie on the side nearest the funiculus. This, the placental haustorium, grows through the integument and funiculus and reaches up to the point of entry of the vascular bundle of the raphe.

An outstanding feature of the embryo in members of Crassulaceae (Mauritzon, 1933; Subramanyam, 1955) is the behaviour of the basal cell of the suspensor. In *Sedum ternatum* and *S. ochroleucum* (Subramanyam, 1955) the basal cell of the suspensor enlarges, becomes vesicular and soon occupies the major portion of the micropylar region of the ovule. Its nucleus becomes very prominently hypertrophied and is surrounded all round by dense granular cytoplasm. It next pushes its way through the nucellar epidermis and now lodges forming a vesicle at the base of the micropylar canal. In *S. ternatum* it grows further in the form of a tube between the nucellar epidermis and the inner integument on the funicular side. In *S. ochroleucum* sometimes the extra nucellar vesicle of the basal cell develops tubiform branches both on the side of the funiculus and the integument. One of these tubes during its further growth crushes the cells of the inner integument and after penetrating through the latter, grows between the inner integument and the raphe. Here it produces a system of haustorial branches and these in turn ramify freely in an intracellular manner through the parenchymatous cells of the raphe, very much resembling the branched hyphae of a fungus mycelium. These haustorial branches are thin-walled and contain granular cytoplasm. Possibly these haustoria developed from the basal cell play a very important part in the nutritional mechanism of the embryo during its growth and further development. The haustorial branches usually penetrate the seed coat. Mauritzon (1933) finds that they

even grow into the funiculus in *S. anopetalum,* while in *S. crassipes* and *Pistorinia hispanica* they come out of the micropyle, thus becoming extra ovular. A similar behaviour of the basal cell is also found in the closely allied families, Podostemaceae (Magnus, 1913) and Hydrostachyaceae (Warming, 1882; Palm, 1915).

An astonishing variety of suspensor organisation is met with in the Orchidaceae (Swamy, 1949). Since the nutritive endosperm tissue is completely suppressed right from the early stage, suspensor haustoria are developed in peculiar ways for drawing nutrition from the surrounding tissues of the seed coat and sometimes even from the placenta. In certain taxa of Orchidaceae the zygote divides by a transverse wall to form two cells, of which the basal again divides transversely so as to result in a proembryo of three cells. The upper cell adjacent to the wall of the embryo sac frequently gives rise to one or more suspensor haustoria which become very prominent and aggressive structures in some species. In a few genera like *Cymbidium* (Swamy, 1942) and *Eulophia* (Swamy, 1943) the zygote may divide by either a transverse or an oblique wall. Further divisions, which do not follow any definite pattern, give rise to a mass of five to ten cells, some of which begin to enlarge enormously and assume a haustorial function. These suspensor cells form long fluffy structures which extend in various directions, piercing the cells of the inner integument and coming into contact with those of the outer one. One or two remaining cells divide transversely to form a filament of variable length whose lower portion gives rise to the embryo proper. In different species of *Habenaria* (Swamy, 1946) a filamentous suspensor, consisting of a variable number of cells is organised. The entire filament elongates out of the embryo sac and micropyle and finally passes out of the outer integument. The free cell reaches the nutritively rich placenta. The nuclei of the suspensor cells become considerably hypertrophied and the plasma stains densely. The free cell finally implants itself in the placenta and penetrates deeply by sending out haustorial processes into the nutritive tissue for absorption of food material. The remaining cells of the suspensor between this free cell and the embryonal mass help in the conduction of nutritive material to the embryo. Thus, the whole structure functions as a true extra-ovular haustorium.

It is thus seen that even during post-fertilisation stages specialised nutritive tissues like the endosperm and perisperm are

organised for supplying nutrition for the developing embryo. In addition to this the suspensor also plays a significant role in the nutritional mechanism of the embryo by developing haustoria in various ways. It may, therefore, be concluded that the nutritional mechanism of the seed is well organised.

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Lilavati—Theory and Design of the "Digito-Analogue" Model III for Solving Six Simultaneous and Secular Equations*

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1. *Introduction*

This paper deals with the theory of a new analogue computer for solving problems involving linear equations, in which data can be fed in and read off as numbers, while the equations themselves are represented by electrical analogies. The circuit used in this computer as the analogue of a linear algebraic form was discussed in two earlier papers by the authors [11] and [7] [(Ramachandran and Krishnamurthy, 1958; Krishnamurthy, 1958)], which also contain an account of two models (Models I and II) capable of solving three linear simultaneous equations. By making use of Ohm's law for multiplication and potentiometric or null setting method for comparing voltages, the circuits can be made to form *exact* analogies of the mathematical problem. This computer has been named Līlāvati, after the title of the well known book on algebra by the Indian mathematician Bhāskarāchārya. The earlier models, however, suffer from the serious disadvantage that the processes employed in them for solving the equations do not necessarily converge in all cases. It therefore becomes necessary to design a computer which is somewhat more versatile, in the sense that it can utilise one or the other of different iterative processes, according to the requirements of the particular problem. The advantage is that, even if one iterative method fails or is slow in a particular case, some other iterative method in which convergence is ensured can be readily substituted, although the latter method would not be commonly used, because it requires a larger

*Part III of the Lilavati series. Parts I and II formed references [11] and [7].

number of operations. Thus it should be readily possible to switch over from one sequence of operations to another, according to the choice of the iterative process. Naturally, this led the authors to a study of the various iterative processes that are available in the literature. A brief survey of the methods that can suitably be mechanised in this computer are given in the next few sections. It will be seen from them that the computer must be capable of performing a variety of sequences. Consequently, the design of the earlier model was so modified that any one of a series of iterative processes could be selected by means of a suitable selector switch, called 'Sequence Selector'. Having selected the sequence, the different steps in an iteration could be performed by setting the 'Step Selector' switch at each of its positions.

A new idea which has been incorporated in this Model III is to have all the data fed in and read as numbers, although the operation of the instrument itself is based on analogue principles. In Models I and II, the coefficients were fed in as resistances in a set of wirewound volume controls, using an auxiliary post-office box arrangement. These volume controls have several disadvantages:

(1) They are not strictly non-inductive and so the operation of the computer with A.C. will not be accurate.

(2) A coefficient which is less than 5 percent of the total value of the volume control cannot be set, if ordinary radio volume controls are used.

(3) The feeding in of the data by means of a standard post-office box arrangement (other types of computers reported in the literature use a standard potentiometer for this) consumes a longer time than even the actual solution of the problem. This is a serious drawback, and also one cannot check up the data by visual examination, after feeding in the data.

(4) Since all the coefficients in a column are in series in a current circuit, the resistance becomes very large and consequently a high voltage power supply is required.

Some of the difficulties, particularly (2) and (3) can be avoided by using accurate Helipot type potentiometers, while difficulties (1), (2) and (3) can be avoided only by using three-decade resistance boxes (for 0·1 % accuracy) but the cost of the computer would then be prohibitive as $n(n+1)$ coefficient potentiometers or resistance boxes would be required.

By making use of a three-decade Kelvin-Varley arrangement of resistances, in which the total resistance is constant, all the four difficulties can be obviated, and further the values of the coefficients can be set as dial readings on a series of decade switches. At the same time, only $(n+1)$ resistance units are required, which brings about a great saving in the number of components and therefore also in the cost. So also, the voltages and currents can be read off as dial readings by making use of potentiometric methods. The basic circuits illustrating the principles are discussed in sections 6, 7 & 8. Fuller constructional details are given in the next paper.

This model of Līlāvati therefore should thus be considered to be a new type of computer* (which may be called "digito-analogue computers"), in which data are fed in and taken out as numbers recorded by dial settings, while the analogy of the mathematical equations is furnished by electrical quantities.

An accuracy of three significant figures is readily possible, which is higher than most pure analogue computers, but of course lower than the purely digital computers. The Līlāvati principle has recently been applied by the authors to the design of a Fourier synthesizer, a polynomial equation solver giving complex roots and related problems like a structure factor computer for x-ray crystallography. Some of these designs are actually being constructed and they will be described in due course.

An advantage of the digital setting of data is that the machine can be made to operate automatically by means of standard telephone uniselectors. The techniques of automatisation are also being worked out and the next Model IV for solving 12 linear equations is expected to be automatic in its operation.

It may be mentioned that the present Model III of Līlāvati is the first analogue machine to be developed in which the various *iterative* processes used in numerical analysis for the solution of both simultaneous and secular equations have been mechanised.

*An altogether different type of digito-analogue computer, using punched cards for programming the problem and parallel high-resistance additive net-work voltage divider circuits for representing the coefficients, has been designed by Walker (1949) [16]. Unfortunately, this work has not been referred to, in several of the publications since that date.

2. *Iterative processes for solving linear simultaneous equations.*

(a) *General theory*: Both direct methods requiring a definite number of operations, as well as indirect or iterative methods, in which the result progressively converges, are available for the solution of these equations. However, only iterative methods are used in general in numerical analysis as they are less laborious and as they do not lead to cumulative errors. Although several such processes have been suggested by various authors, no unified approach to the problem appears to have been given so far. Therefore, a general treatment of the problem is given here and the various types of iterative processes are then considered as particular cases of the general method.

The set of n linear simultaneous equations

$$\sum_{j=1}^{n} a_{ij}x_j = g_i,\ i = 1 \text{ to } n \qquad \ldots (1)$$

can be put in terms of matrix notation in the form

$$AX = G \qquad \ldots (2)$$

$$\text{or, } G - AX = O \qquad \ldots (3)$$

In any iterative process, an arbitrary set of numbers $x_i^{(1)}$, $i = 1$ to $n (\equiv X^{(1)})$ are chosen and fed into Eqn. (3) which will in general not be satisfied by these numbers.

$$\text{Let } G - AX^{(1)} = R^{(1)} \qquad \ldots (4)$$

where $R^{(1)} \equiv r_i^{(1)}$ are the residuals.

The essential idea in an iterative process is to feed back the residuals into the x_i's so as to get a better approximation to the solution. The most general linear relation possible between the fed back values and $R^{(1)}$ is of the form

$$X^{(2)} - X^{(1)} = \triangle X^{(1)} = -BR^{(1)} \qquad \ldots (5a)$$

$$\text{where } \triangle x_i^{(1)} = x_i^{(2)} - x_i^{(1)} \qquad \ldots (5b)$$

and B is a $n \times n$ matrix. The negative sign is chosen in Eqn. 5 (a), for convenience. It also emphasises the idea of negative feed back.

$$\text{Now let } G - AX^{(2)} = R^{(2)} \qquad \ldots (6a)$$

This is again fed back to give

$$X^{(3)} = X^{(2)} + \triangle X^{(2)} = X^{(2)} - BR^{(2)} \quad \ldots \quad (6b)$$

and the whole process is continued until all the residuals are less than the required limits of error. Thus the iterative process is defined by the two equations

$$X^{(p+1)} - X^{(p)} = \triangle X^{(p)} = - BR^{(p)} \quad \ldots \quad (7a)$$

and $$G - AX^{(p)} = R^{(p)} \quad \ldots \quad (7b)$$

Now, the condition for the process to converge is that $R^{(p)} \to 0$ as $p \to \infty$. From Eqn. 7(a) and (b), it follows that

$$R^{(p+1)} = (I + AB)R^{(p)} = MR^{(p)} \quad \text{(say)} \quad \ldots \quad (8)$$

A sequence of vectors $R^{(p)}$ definited by the iterative formula Eqn. (8) converges if all the eigenvalues of the matrix $M = (I+AB)$ are of modulus less than unity (see Appendix II). This therefore is the condition for convergence of any iterative process defined by Eqns. 7(a) and 7(b).

(b) *Particular cases*: We shall first consider briefly the iterative processes available in the literature.

(i) *Relaxation process*: In the familiar relaxation process [15] (Southwell, 1940) one adjusts the unknowns suitably, depending upon the skill of the computer, to decrease the residuals continuously until they all become zero. No definite rules are given for this purpose and in terms of our notation it is equivalent to guessing the elements of the matrix B at each step. In view of the absence of definite rules this method is not suited for mechanisation, although it can be performed in the computer.

(ii) *Gauss-Seidel process*: This is the process that was adopted in the Models I and II. It is the simplest of all the available methods, as far as mechanisation is concerned, and works in a large majority of cases.

The process can be readily shown to be equivalent to choosing the matrix B to be $-A_1^{-1}$ where A_1 is the triangular matrix containing all elements of A which occur on the leading diagonal and to the left of it. Making this substitution for B in Eqn. 7(a), one obtains the iterative formula $A_1X^{(p+1)} + A_2X^{(p)} = G \quad \ldots \quad (9a)$

where $A_1 + A_2 = A \quad \ldots \quad (9b)$

The matrix M of Eqn. (8) is now equal to $A_1^{-1} A_2$ and so, the condition for convergence is that the pth power of this matrix should tend to zero as $p \to \infty$. This would be so if $N(M) < 1$ where $N(M)$ is the norm of the matrix M (Berry, [2] 1945), but a more useful condition, which is both necessary and sufficient, is that all its eigenvalues are of modulus less than unity (Appendix II). The calculation of the matrix $M = A_1^{-1} A_2$ is quite a laborious process and so this criterion is not useful for testing whether the process would converge for a given matrix A. In fact, the exact conditions on the matrix A which would ensure that this process converges do not seem to have been worked out so far, although some conjectures have been made, some of which are found to be not valid. Some sufficient conditions for convergence have been worked out by the authors and are given in Appendix III.

(iii) *Zadunaisky's method*: Zadunaisky's method [19] (Zadunaisky, 1958) also consists in dividing the matrix A into two parts, A_1 and A_2, and using the iterative process of Eqn. 9(a), but A here consists only of the diagonal terms of A, with all the other elements zero. The condition for convergence is more easily computed in this case, since A_1^{-1} in the product $A_1^{-1} A_2$ is again a diagonal matrix. However, this has no greater advantage over the Gauss-Seidel process, for convergence depends on the matrix A, and there is no way of ensuring it.

(iv) *Cesari's method*: Cesari's method (Reported in [19] Math. Revs. *19*, 175) consists in taking B as any general non-singular matrix. But as there are no definite rules as to the choice of B, it is only of academic interest.

(v) *Morris method*: In the Morris iterative method, described in Frazer, Duncan and Collar [3] (1950), the matrix A is taken as a sum of two matrices A_1, A_2, where A is taken to be an easily invertible matrix, preferably a triangular or unit matrix. It might be possible to ensure convergence of M^p in this case by a suitable choice of A_1, but the exact conditions for this have not been worked out.

(c) *Solution of simultaneous equations with complex coefficients.*

A set of n linear simultaneous equations in n complex variables is equivalent to a set of 2 n equations in 2 n real variables, all with real coefficients. Consequently, the solution of complex

equations leads to no new problem, except that a machine designed to solve $2n$ real equations can only solve n complex equations. Otherwise, all the methods mentioned above can be used, with appropriate modifications.

3. *The Richardson-Hotelling Process*:

The method to be discussed below (which may be called the RH Process) was first proposed by Richardson [12] (1910) in connection with the solution of differential equations and was considered in more detail by Hotelling [6] (1943). It has been incorporated in a computer by Mitra [10] (1955), but the conditions for its convergence do not appear to have been fully worked out previously.

These are best discussed with reference to the general treatment given in the last section. If we take the feed-back matrix B to be the diagonal matrix $-I/b$, where b is a numerical parameter, then

$$X^{(p+1)} - X^{(p)} = \triangle X = \frac{R^{(p)}}{b} \qquad .. \quad (10)$$

and the iterative process is defined by the sequence

$$(A - bI)X^{(p)} - G = -bX^{(p+1)} \qquad .. \quad (11)$$

In the iterative process described by Eqn. (11), the matrix M becomes equal to $I - A/b$ and the eigenvalues of this matrix can be immediately worked out in terms of the eigenvalues of the original matrix A. If the latter are λ_k then those of M are

$$\lambda'_k = 1 - \lambda_k/b \qquad .. \quad (12)$$

(a) *Condition for convergence*:

As is well known, the eigenvalues of a matrix can be complex numbers and in an Argand diagram, the condition that all $|\lambda'_k|$ are < 1 may be represented by the condition that all the eigenvalues of A must lie within a circle whose radius is b times that of the unit circle, and located as shown in Fig. 1, with its centre at (b, O). Such a condition is obviously impossible to have if the matrix A is quite general. On the other hand, if the eigenvalues of A are all real and positive, then it is only necessary to have $b > \lambda_1/2$, where λ_1 is the largest of them, to satisfy this condition.

Thus it follows that one can always ensure convergence for the solution of any problem by the sequence given by Eqn. (11), by making a proper choice of the parameter b, provided the matrix A has eigenvalues which are real and positive.

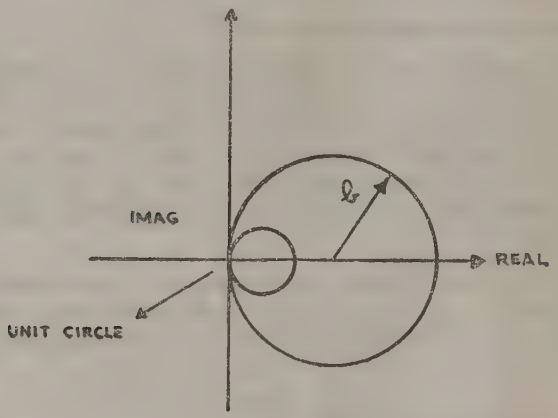


FIG. 1: Convergence criterion

The last condition is equivalent to saying that the matrix A must be positive definite. However, even if it is not so, one can reformulate the problem, $AX = G$, by choosing a new set of variables Y, related to the set X by the equation

$$X = A^{+}Y$$

A^{+} being the Hermitian conjugate of A, so that

$$AA^{+}Y = HY = G \qquad .. \quad (13)$$

Here H is necessarily positive definite. Hence the solution of Eqn. (13) can always be made to converge by the process described above. Having obtained Y, X can then be obtained from Y, by multiplying with the matrix A^{+}, which is a straightforward process. (In particular if A is a general real matrix, then the matrix $H = A\tilde{A}$). An alternative method is to multiply both sides of the equation $AX = G$ by A^{+} and obtain

$$A^{+}AX = A^{+}G \text{ or } H'X = F \qquad .. \quad (14)$$

where F is known, so that X can be directly solved for.

The iterative process (11) is therefore universally applicable to the solution of any set of linear simultaneous equations, (including those with complex coefficients), by choosing a suitable value for the real parameter b. The value of λ_1, the largest eigenvalue of the matrix A, required for making this choice can readily be obtained by a simple process to be described in section 5.

(b) *Speed of convergence*:

Although any value of $b > \lambda_1/2$ ensures convergence, the speed of convergence depends on its actual value. It can be shown that the best choice of b, for maximum convergence, is $b = (\lambda_1 + \lambda_n)/2$ where λ_n is the least on the eigenvalues. A good approximation to λ_n can again be obtained quickly, if necessary (see section 5).

In practice, however, unless λ_1 and λ_n are widely different, good convergence is ensured by any value of b slightly larger than $\lambda_1/2$. If $\lambda_n \leqslant \lambda_1$, i.e., the ratio $\lambda_1/\lambda_n \geqslant 1$ then the convergence is always slow. On the other hand, if all the eigenvalues are closely clustered and $|\lambda_i - \bar{\lambda}|/|\bar{\lambda}| \leqslant 1$ where $\bar{\lambda}$ is the mean of the eigenvalues, then this method is very fast.

(c) *Relation to eigenvalue problem*:

It is also interesting to note that the process discussed in this section is exactly the same as what would be used to find out the eigenvector of the $(n+1) \times (n+1)$ matrix C given by

$$\mathbf{C} = \left(\begin{array}{c|c} \mathrm{A}\,(n \times n) & -\mathrm{G}\,(n \times 1) \\ \hline 0\,(1 \times n) & 0 \end{array} \right)$$

corresponding to the least root zero. In practice, as it cannot be determined directly, this matrix is modified to

$$\mathbf{D} = b\mathbf{I} - \mathbf{C} = \left(\begin{array}{c|c} b\mathrm{I} - \mathrm{A} & \mathrm{G} \\ \hline 0 & b \end{array} \right)$$

The corresponding eigenvector $\mathbf{X}$ of $\mathbf{D}$ now corresponds to its largest eigenvalue b, and it can be determined by using the familiar matrix power iterative process,

$$\mathbf{D}\mathbf{X}^{(p)} = b\mathbf{X}^{(p+1)} \qquad \ldots \quad (15)$$

as proved in the next section. In the first n terms of the vector $\mathbf{X}$ are identified with the vector X of Eqn. (2), then Eqn. (15) is readily seen to be equivalent to the earlier Eqn. (11).

(d) *Relation to least-squares method:*

Adcock [1] (1948) has mechanised a least-square method for the solution of simultaneous linear equations. It can be shown that this process is identical with the RH-process applied to Eqn. (13).

4. *Conditions for convergence of the Gauss-Seidel Process.*

(a) *Criterion for convergence:*

The Gauss-Seidel process (for short GS process) has been described in the earlier parts, and its matrix representation is given by Eqns. 9(a) and (b). This is a process which has been very widely used and discussed in the literature and yet no precise results seem to be available as to the conditions for its convergence and as to the speed of convergence.

However, it is possible to show (as in Appendix III), that the process always converges if the matrix A is Hermitean and positive definite, or symmetric and positive definite in the case of real matrices.

It is interesting to note that the matrices H and H′ of the previous section, namely AA^+ and A^+A respectively, both satisfy these conditions, so that the corresponding equations (13) and (14) converge as surely under the GS process as under the RH process.

However, if A is positive definite, but not symmetric, then the RH process can be made to converge by a suitable choice of b, but the GS process need not converge. It will be obvious from Appendix III that a sufficient condition for it to converge under the GS process is that both A and the matrix $(A_1 - \tilde{A}_2)$ must be positive definite.

If A itself is both Hermitean and positive definite, then it can be put in the form $A = C^+C$ and so whatever was said above for H holds for A also.

It must be emphasized that the above are only *sufficient* conditions and that they may not be necessary. In fact, the solutions of most equations (represented by non-symmetric matrices A) do converge under the GS process. So far it has not been possible

to work out the necessary conditions. However, this is not a serious disadvantage in the practical solution of problems, for the following definite steps can be suggested for any problem:

(i) Try the GS process with the original matrix itself. For most problems this would converge.

(ii) If this does not converge, then reformulate the problem in terms of the matrix $H = AA^{-}$ or $H' = A^{+}A$. In either case, the solution of the reformulated problem will converge under the GS process.

(b) *Speed of convergence*:

Unlike for the RH process, it has not been possible to work out the exact conditions for rapid convergence. It will be noticed that there is no variable parameter here, so that the speed of convergence would depend on the matrix A itself. Several conjectures have been made in the literature regarding the criterion for a set of equations to be "ill-conditioned" or not. Some of these are, however, found to be invalid, when tried on examples. For instance, it seems to be the general impression that if $|\lambda_{max}|/|\lambda_{min}|$ of the matrix A is large, then the equations are ill-conditioned (Hartree, [5] 1952). In fact, a set of 4 equations proposed by Wilson quoted by Hartree, [5] (1952) has for this ratio the value $29{\cdot}7/0{\cdot}7 \simeq 42$ and in fact it does converge only very slowly. Actually the authors found that even 30 iterations, the result was still not accurate (1·69, 0·6, 0·81, 1·10) as against ($x_1 = x_2 = x_3 = x_4 = 1$). However the authors have been able to set up the following set of 5 equations (Eqn. 16), for which the ratio $|\lambda_{max}|/|\lambda_{min}|$ is even larger, namely $\simeq$ 400 ($\lambda_{max} = 1{\cdot}2$; $\lambda_{min} = 0{\cdot}003$) and yet the solution converged in 5 cycles under the GS process. However, it did converge only very slowly under the RH process, as it should.

$$\begin{bmatrix} 1{\cdot}000 & 0{\cdot}170 & 0{\cdot}060 & -0{\cdot}070 & -0{\cdot}030 \\ 0{\cdot}170 & 0{\cdot}940 & 0{\cdot}075 & -0{\cdot}200 & -0{\cdot}040 \\ 0{\cdot}060 & 0{\cdot}075 & 0{\cdot}630 & 0{\cdot}020 & -0{\cdot}013 \\ -0{\cdot}070 & -0{\cdot}200 & 0{\cdot}020 & 0{\cdot}470 & 0{\cdot}000 \\ -0{\cdot}030 & -0{\cdot}040 & -0{\cdot}013 & 0{\cdot}000 & 0{\cdot}006 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \end{bmatrix} = \begin{bmatrix} 1{\cdot}09 \\ 1{\cdot}28 \\ 2{\cdot}11 \\ 1{\cdot}47 \\ -0{\cdot}12 \end{bmatrix} \quad .. \quad (16)$$

A further discussion of ill-conditioned equations will be given later.

5. *Iterative processes for secular equations:* *

The secular equation for an $n \times n$ matrix A, takes the form

$$\Sigma_j \, a_{ij}x_j = \lambda x_i \quad (i = 1 \text{ to } n) \qquad .. \quad (17a)$$

$$\text{or } AX = \lambda X \qquad .. \quad (17b)$$

It is well known that this equation has solutions only for certain values of λ say λ_k, which are known as the eigenvalues of the matrix. The corresponding solution $X_k \, (\equiv x_i^{(k)})$ is called the eigenvector pertaining to this eigenvalue. Obviously any multiple of X_k is also an eigenvector corresponding to the same eigenvalue. But in practice, as we are interested only in the relative ratios of the components of X, it is customary to choose $x_1^{(k)}$, or any one of the $x_i^{(k)}$'s to be unity. When the largest of the x_i's is made unity, we shall call it as the "standardised form" of the eigenvector.

The number of distinct eigenvalues and eigenvectors can at most be equal to n, the order of the matrix. Some of the eigenvalues may be repeated, in which case the number of distinct eigenvalues m, is less than n.

It will be noticed that Eqns. (17) are very similar in form to the set of simultaneous equations (2), so that the basic circuits of Līlāvati could be readily utilised for solving these equations. This is particularly so if the quantities entering Eqn. (17a) are all real.

In fact, the secular equations which occur in physical problems are generally concerned with vibrations of a system, and in all these cases, the matrix A is real and symmetric. The eigenvalues in such a case are also real and so are all the components of the eigenvectors. The discussion below will therefore be restricted to real symmetric matrices.

This computer can also be used for determining complex eigenvalues of real matrices by a method described by [17] Wilkinson (1954). However, if the matrix itself is complex, further facilities are required in the computer. These will not be discussed here. The following is a brief account of the iterative

* For proofs of the unproved statements made in this section, reference may be made to standard works on matrices and numerical analysis.

methods* which appear to be most suitable for adaptation in Līlāvati.

(a) *General discussion*: When the number of eigenvectors is equal to the order of the matrix (n) it is possible to expand any arbitrary vector X defined by the set of numbers $x_1, x_2, \ldots\ldots x_n$, in terms of the eigenvectors in the form

$$X = \Sigma\, \alpha_k X_k \qquad \ldots\ldots (18)$$

This expansion theorem is valid for all matrices which can be diagonalised. This includes besides other (a) matrices for which all the eigenvalues are different, and (b) the so called 'normal' matrices, which satisfy the equation $AA^{+}=A^{+}A$. The latter class includes Hermitean, Anti-Hermitean and unitary matrices, whose real counterparts are symmetric, antisymmetric and real orthogonal matrices. However, not even all real matrices possess this property. In fact, the number of distinct eigenvectors, t, is less than or equal to n, the order of matrix, in the general case [14] (Schmeidler, 1949). (Appendix I).

(b) *Largest eigenvalue*: We shall suppose that the eigenvalues are arranged in decreasing order of magnitude such that

$$|\lambda_1| > |\lambda_2| > \ldots\ldots |\lambda_n|$$

It can be readily shown that if one successively multiplies an arbitrary vector X by the matrix A, then the result converges in the limit to the eigenvector X_1, corresponding to the largest eigenvalue λ_1. Thus if $X^{(p)}$ is the value of the standardised vector at the pth stage, i.e., $X^{(p)} = A^p X$ and $\lambda^{(p)}$ is the ratio $x_1^{(p+1)}/x_1^{(p)}$ then $X^{(p)} \to X_1$ and $\lambda^{(p)} \to \lambda_1$ as $p \to \infty$. This follows from the expansion theorem, for at each step, the proportion of X_1 in X goes on increasing. Even when the eigenvalues are repeated, it can still be shown that this process leads to the largest eigenvalue and an eigenvector corresponding to this eigenvalue. This follows from Appendix II. The rate of convergence of this process depends on the ratio $|\lambda_1|/|\lambda_2|$ being faster the larger is the ratio.†

* A relaxation process has already been mechanised, [4] and [7], and will not be dealt with here.

† If two or more of the eigenvalues have the same modulus $|\lambda_1|$ then this process will not converge, but will lead to repeating cycles for $X^{(p)}$. When this happens, one can take the matrix $(A - \mu I)$ where μ is some number, for which the corresponding eigenvalues will not be equal.

(c) *Least eigenvalue*:

Having determined λ_1, the largest eigenvalue, the method of obtaining the least one is to use the same process as above, but use the matrix $(A - \lambda_1 I)$ instead of A. This matrix has eigenvalues $\lambda'_k = (\lambda_k - \lambda_1)$ where λ_k is the corresponding eigenvalue of A, and of these, λ'_n is obviously the largest in magnitude. If X_n is this vector, then

$$(A - \lambda_1 I) X_n = (\lambda_n - \lambda_1) X_n$$

$$\text{or } AX_n = \lambda_n X_n$$

so that X_n is also the eigenvector of A, corresponding to the root λ_n.

(d) *Intermediate eigenvalues*:

Since any vector X can be written as $X = \Sigma \alpha_k X_k$ it is obvious that $Y = (A - \lambda_1 I) X$ will be independent of X_1 the first eigenvector. Consequently $A^p Y$ will converge to the next largest eigenvalue and the corresponding eigenvector. If λ_1 is not repeated, these would obviously be λ_2 and X_2. If on the other hand λ_1 is repeated and the matrix A is diagonalisable (as is the case with real symmetric matrices), then this would again be λ_1, but the vector will be different (orthogonal to X_1).

This process of obtaining Y free of X_1 is called a purification process (Richardson, [13] 1950). It could be readily employed in the computer and if at any stage, during successive multiplication by A, the process is found to diverge, i.e., it tends to go towards λ_1, the purficaton process has to be repeated.

This method can obviously be continued to obtain still lower eigenvalues. To get the kth eigenvalue (say), the arbitrary vector X has first to be multiplied by $(A - \lambda_1 I)(A - \lambda_2 I) \ldots\ldots (A - \lambda_{k-1} I)$ and then the successive multiplications by original matrix A have to be carried out. Also at intermediate stages, if there is divergence towards higher eigenvalues, purification has to be repeated.

There are other processes described for getting the lower eigenvalues (Hartree [5] (1952), Wilkinson [17] (1954) Wilson, Decius, and Cross [18] (1955)). These methods are (1) deflation method, and (2) orthogonalisation method. The deflation method is based on the expansion of a symmetric matrix A as

$\sum_k \lambda_k X_k \tilde{X}_k / \sum_{i=1} x_i^{(k)2}$ where λ_k is the kth eigenvalue and $\tilde{X}_k$ is the transpose of X_k, the eigenvector corresponding to the eigenvalue λ_k for the matrix A. In this method, having determined the value of λ_1, the new matrix $A^{(1)}=A-\lambda_1 X_1 \tilde{X}_1 / \sum_{i=1}^{n} x_i^{(1)2}$ is formed. This will have roots $0, \lambda_2, \ldots . \lambda_n$. Therefore convergence to λ_2 can be obtained by repeated multiplication by $A^{(1)}$. However as errors in $A^{(1)}$ will lead to cumulative errors in succeeding stages, this method will not be accurate.

The orthogonalisation method consists in making each new vector, at any stage, to be orthogonal to the first eigenvector and so on, the obtaining the convergence to the respective eigenvalues.

6. *Basic steps in the various iterative processes and their analogies.*

The various methods discussed above for solving simultaneous and secular equations all require only two types of basic operations, which may be called

(a) Matrix multiplication

and (b) Transfer of data.

The operation of matrix multiplication may be represented by the equation

$$AX = G \text{ or } AX - G = 0$$

which becomes in detail

$$\sum_j a_{ij} x_j - g_i = 0 \quad (i = 1 \text{ to } n) \qquad \ldots \quad (19)$$

The analogy of this equation requires $(n+1)$ columns and n rows. The essential idea is to vary either one of the x_j's or the g_i's so as to obtain zero. In the Gauss-Seidel process, the former is done, while in simple matrix multiplication, g_i is obtained in this way. Some of the steps in the other iterative processes are also of this type, with a small extension. Thus the equation

$$(A-bI)X^{(p)} - G = -bX^{(p+1)} \qquad \ldots \quad (11)$$

can be written in the form

$$A'X^{(p)} - G + R^{(p)} = 0 \qquad \ldots \quad (20a)$$

and

$$X^{(p+1)} = R^{(p)}/b \qquad \ldots \quad (20b)$$

where A', G and $X^{(p)}$ are known and $X^{(p+1)}$ has to be found out, which is done in two steps.

The step 20(a) requires $(n+2)$ columns and n rows, but otherwise the basic arrangement is the same as that for the matrix multiplication. The step 20(b) requires the transfer of the result in the previous step, with a multiplying factor $1/b$.

So also, in solving secular equations and the subsequent standardisation of the eigenvector (i.e., making one of the components unity) the same two types of basic operations are involved, as in the following Eqns. 21(a) and (b) which are exactly similar to Eqns. 20(a) and (b).

$$AX^{(p)}+R^{(p)}=0 \quad .. \quad (21a)$$

$$X^{(p+1)}=-R^{(p)}/\lambda \quad .. \quad (21b)$$

(a) *Analogy of matrix multiplication:*

The block diagram of the arrangement for this is shown in Fig. 2(a) and the circuit diagram for a simple two-equation example of Eqn. (20a) is shown in Fig. 2(b). The quantities marked at the top of Fig. 2(b) are the currents through the various circuits, and the quantities marked against the resistances are their values.

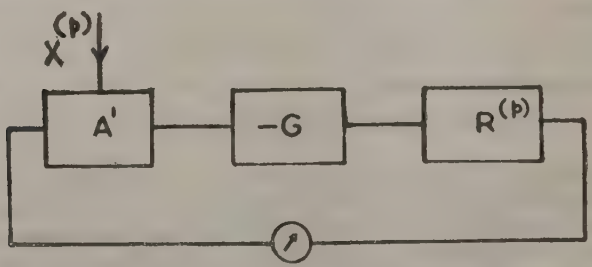


Fig. 2(a): Analogy of a matrix multiplication

(b) *Transfer of data (Feed-back):*

The block diagram of the arrangement corresponding to the equation $X^{(p+1)}=R^p/b$, where b is given, is shown in Fig. 3(a). The detailed circuit diagram is shown in Fig. 3(b). The current through $r_1^{(p)}$ and $r_2^{(p)}$ which was originally unity is changed to $1/b$, the multiplying factor, and the transfer is done by effecting

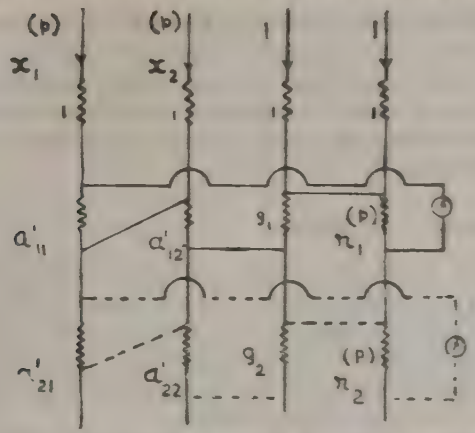


FIG. 2(b): Two-equation analogy for matrix multiplication

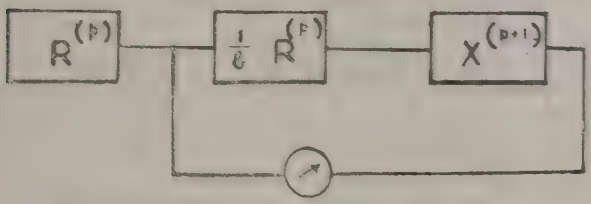


FIG. 3(a): Analogy of transfer

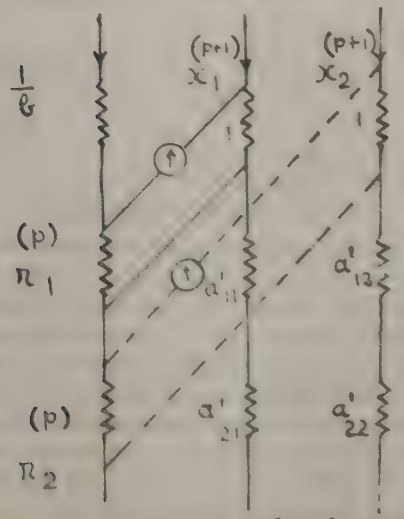


FIG. 3(b) Two-equation analogy for transfer

the diagonal connections shown in Fig. 3 (b). It should be mentioned that the circuit diagrams in Figs. 2 (b) and 3 (b) are intended only to clarify the ideas. Actually in the computer they are arranged in an entirely different way, as will be clear from the succeeding sections, and from the next paper dealing with the constructional details.

7. *The Kelvin-Varley Bridge*:

In models I and II, separate resistances were used to represent each of the coefficients a_{ij}. As mentioned earlier, by using the Kelvin-Varley arrangement, it is possible to have only $(n+2)$ resistance boxes from which the appropriate values of a_{ij}, g_i and r_i corresponding to each row can be tapped and connected up as required by means of selector switches.

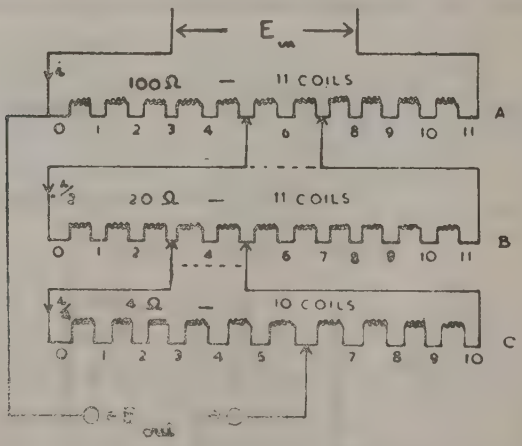


Fig. 4: Kelvin-Varley Bridge

The Kelvin-Varley arrangement of resistance providing a three decade range in value is shown in Fig. 4. The top row consists of eleven coils each of resistance r ohms. Connected across two of these coils is another row of eleven coils, each of resistance $r/5$ ohms, the shunting connections being made through two sliding contacts which always move together, so that two coils of resistance 2 r in the upper row are shunted by the total resistance 2 r in the row below, at each step. Again two of the coils in this second row are shunted in the same way by a series of ten coils whose total resistance is equal to that of the two coils which it

shunts, namely $2r/5$ ohms. Since in each case the two coils are shunted by a resistance equal to their own resistance, the resistance of the combination is the same as the resistance of one coil, so that the total effective resistance of each of the rows in the system is in each case that of ten coils only and the total effective resistance of the system across the points connected to the input (E_{in}) is always $10r$, irrespective of the settings of the contacts. On the other hand, the output E_{out} can be made equal to any integral multiple of $0{\cdot}001\ E_{in}$ (from 0 to 1000) by suitably setting the three decade switches A, B and C. The dial readings of these switches would give straightaway the three digits of the number represented by E_{out} if $0{\cdot}001\ E_{in}$ is taken as the unit. On the other hand, irrespective of the settings of these switches, the total resistance of the box is a constant, and so the current flowing through the box does not vary with the switch settings.

The number of rows in the Kelvin-Varley arrangement can be made as large as one likes, by continuing the same principle, and so this arrangement is an ideal potentiometer in which the output voltage can be set to any value correct to the desired number of significant figures. The only limitation is the contact resistance of the switches, which are contained in the current-bearing circuit.

In the arrangement used in our computer r is 100 ohms, so that the total resistance is 1000 ohms. The accuracy of each of the coils used was 0·1%.

8. *The Selector Switches*:

(a) *The step selector*: In order to mechanise the various processes it is enough if we set up the analogy of a single equation at a time. Consequently, the data for all the n equations can be fed in by making use of n groups of switches for each box, to which the potential points of the particular potentiometer are all brought. The arrangement for one of the boxes (say box 1) is shown in detail in Fig. 5. The points A_{i1}, A'_{i1} are the two poles of a 2 pole 10 way switch, A_{i1} having the ten ways connected to the points 0-9 and A'_{i1} having its ten ways connected to the points 2-11 of the series of coils in the row A of the Kelvin-Varley Bridge in the first box. B_{i1} and B'_{i1} are similar poles of a 2 pole 10 way switch having their ten ways connected to the points 0-9 and 2-11 respectively of the series of coils in the second row B. C'_{i1} is the pole of a 1 pole 11 way switch having its ways connected to the points 0-10 of the third series of coils in the row C.

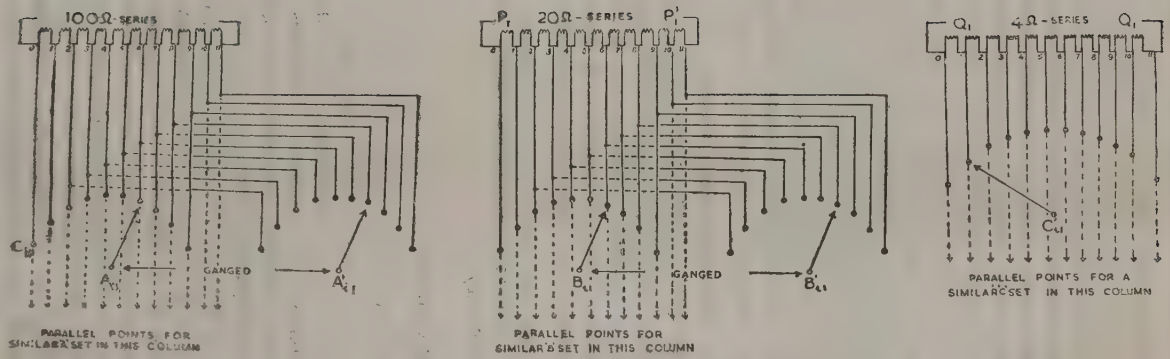


Fig. 5: Three decade set-switches for a column.

Exactly similar connections are made to $(n-1)$ other series of three decade switches (single pole or double pole switches as the case may be). Thus, n sets of switches, arranged in a vertical column, have their ways all connected in parallel to the various points of the first box, as described above.

Similarly, each of the boxes (there are $(n-1)$ boxes in our computer) is connected up to n sets of 3 switches arranged in a vertical row. Thus there are n $(n+1)$ sets each consisting of three setting switches, arranged in a rectangular array, for the representation of the coefficients. Since the present Model III is designed to solve six equations, by the Gauss-Seidel method, (and five equations by RH Process) there are 6 rows and 7 columns in the computer.

The purpose of the step selector is to connect up the poles of the three decade switches, representing each one of the coefficient in a column, to the end terminals of the corresponding resistance box and add up all the resulting voltages, corresponding to a row, through plus-minus switches, as in the earlier models. Thus the analogy of $\sum_{j=1}^{n} a_{ij} x_j$ is set up for the first setting of the step selector and this is connected to g_i with the opposite sign through the galvanometer. The analogy of each row at a time is thus set up in the n settings of the step selector. This corresponds to the matrix multiplication process, discussed in section 6.

For transfer of data, at each setting of the step selector switch one of the picked out voltages from a particular column (which may conveniently be arranged to be the last or the $(n+1)$th column) is compared with the voltages across unit resistance in one of the columns. In the design of Model III, separate selector switches are used for the two purposes. Which of these processes (matrix multiplication or transfer of data) is done is predetermined by a sequence selector switch to be described below.

(b) *The Sequence Selector*:

This switch determines the interconnections made by the step selector between the several voltages picked out, for adding in series. If this switch is set in the matrix multiplication position, or the Gauss-Seidel process, which also requires the same connections, all the picked out voltages are connected in series, a current

unity is made to flow in the $(n+1)$th column and the galvanometer brought to the right position for balancing. If this switch is set in the feed-back position, i.e., for transfer of data, the galvanometer is brought for comparison of voltages in the various rows of the $(n+1)$th column with the voltage developed across unit resistance in each of the columns. The current through the $(n+1)$th column is changed to $1/b$ if a multiplication by such a factor is required, as in Eqn. 20(b). The same arrangement is also used for measuring the current in each one of the columns, but now the current through the $(n+1)$th column is made equal to unity.

Further details regarding the design and construction are reserved for Part IV of this series.

9. *Acknowledgements*:

The authors wish to thank Messrs. V. R. Sambandam, and T. Shanmugam of this department, for their help in the construction of this computer.

SUMMARY

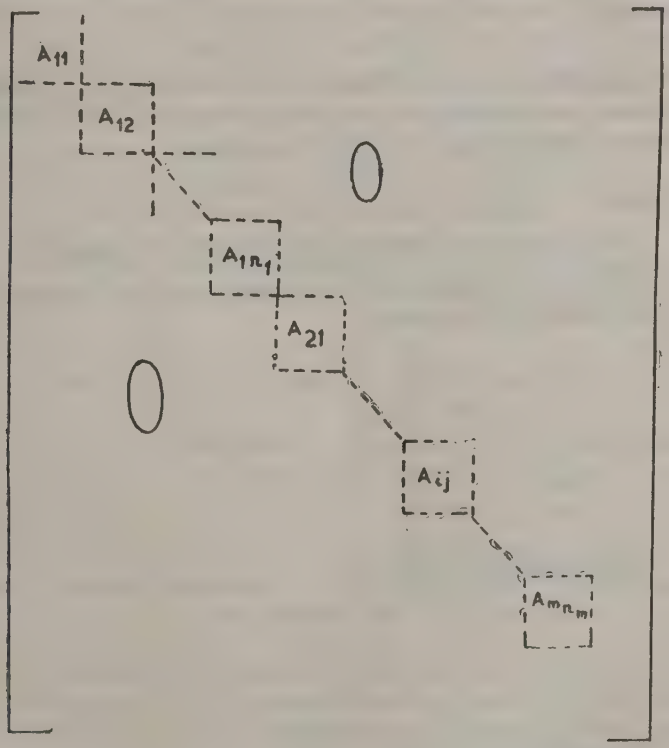
This paper describes the general principles involved in the design of Model III of Līlāvati, an analogue computer for solving both simultaneous and secular equations by a variety of iterative methods.

Several new features are introduced in this model. Firstly, by using a Kelvin-Varley arrangement of resistances, the data can be fed in and read off as three digit numbers. At the same time only one row of resistance boxes is required, the analogy of each row in turn being obtained by suitable ganged switches incorporated in the so-called "Step Selector". The instrument is also designed so as to work on a variety of iterative processes, and going over from one process to another can be done by changing the setting of another set of ganged switches, the "Sequence Selector".

Model III is designed to solve simultaneous equations or secular equations in six unknowns. A brief review of the various iterative processes available for this purpose is also given, together with the conditions for their convergence.

APPENDIX I

A Hermitean matrix or a real symmetric square matrix, of order n, has n distinct eigenvectors, which are all linearly independent. Consequently the expansion theorem (Eqn. 18 of Sec. 5) holds in these cases. The conditions for the occurrence of such a complete set of independent eigenvectors for a general matrix do not appear to be clearly stated in the literature. It is the purpose of this appendix to clarify some points connected with this.



It is well-known that any matrix M can be transformed to the diagonal from A by the transformation of the type $A = S\,M\,S^{-1}$ if all its eigenvalues are different. When some of the eigenvalues are repeated, it can only be transformed to the above 'canonical' form [8] (see e.g., Littlewood, 1950, p. 13).

where each submatrix A_{ij} is of the form

$$A_{ij} = \begin{bmatrix} \lambda_i & 1 & 0 & 0 & \ldots & 0 \\ 0 & \lambda_i & 1 & 0 & \ldots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & 0 & \ldots & \lambda_i \end{bmatrix}, \text{ order } s_{ij}$$

Thus the canonical form can be split up into blocks, such that when any vector X is multiplied by A, the vector also can be considered to be divided into corresponding blocks and only elements formerly in a block occur in the corresponding block of the product AX. As a consequence, it is possible to deduce all the properties of A by first considering those of one of the blocks.

Also, since equivalent matrices have the same characteristic equation and otherwise have the same properties, it is enough to consider the canonical form for this purpose.

Lemma

Each block of the canonical form has only one eigenvector.

Proof: Take the matrix A_{ij} of order s, and let its eigenvector X be defined by the equation

$$\begin{bmatrix} \lambda & 1 & 0 & \ldots & 0 & 0 \\ 0 & \lambda & 1 & \ldots & 0 & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ \cdots & \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & \ldots & \lambda & 1 \\ 0 & 0 & 0 & \ldots & 0 & \lambda \end{bmatrix} \begin{bmatrix} a \\ b \\ \cdots \\ \cdots \\ g \\ h \end{bmatrix} = \lambda \begin{bmatrix} a \\ b \\ \cdots \\ \cdots \\ g \\ h \end{bmatrix}$$

It immediately follows that

$$\begin{aligned} \lambda a + b &= \lambda a \\ \lambda b + c &= \lambda b \\ &\cdots\cdots\cdots \\ \lambda g + h &= \lambda g \\ \lambda h &= \lambda h \end{aligned}$$

so that $h = g = \ldots = b = 0$, and only $a \neq 0$. Hence the only eigenvector is in the normalised standardised form, $\begin{pmatrix} 1 \\ 0 \\ \cdots \\ 0 \end{pmatrix}$. There are no other eigenvectors.

This can be generalised to the following result.

Theorem 1. The number of eigenvectors corresponding to $\lambda_1, \lambda_2, \ldots$ are $r_1, r_2, \ldots$ where $r_1, r_2, \ldots$ are the number of blocks in the canonical form corresponding to these eigenvalues. The eigenvectors have 1 in the row corresponding to the top row of the relevant block and zero elsewhere.

Theorem 2 follows from this.

Theorem 2. The number of distinct eigenvectors of a matrix, satisfies the inequality

$$n \geqslant t \geqslant m$$

where n is the order of the matrix and m is the number of distinct eigenvalues.

The number t is obviously equal to the total number of block occurring in the canonical form. When $t = n$, all the blocks are of order 1, and the canonical form is purely diagonal.

The condition for diagonalisability can again be obtained from the canonical form. It is obvious that the block A_{ij} satisfies the equation

$$(A_{ij} - \lambda_i I)^{s_{ij}} = 0 \text{ but not } (A_{ij} - \lambda_i I)^{(s_{ij}-1)} = 0.$$

Since the blocks are independent, as stated above, it follows that s_{ij} must all be equal to unity if all the submatrices are to be of order one. Hence,

Theorem 3. The necessary and sufficient condition that a matrix M can be diagonalised is that it satisfies the minimal equation of degree m, viz., $(M-\lambda_1 I)(M-\lambda_2 I) \ldots (M-\lambda_m I) = 0$.

Unfortunately this theorem is of no help in testing whether a matrix is diagonalisable or not. The only known result which is useful for such a test is the sufficient condition, namely that the matrix is normal, i.e., $MM^* = M^*M$ (MacDuffee [10] 1956, p. 76). In this case, it can be diagonalised by a unitary transformation.

It is also obvious that when all the eigenvalues are different, the characteristic equation is itself the minimal equation and hence the matrix can be diagonalised.

APPENDIX II

Here we shall consider the conditions for the convergence of A^p to the null matrix as $p \to \infty$. Again, it is sufficient to consider the canonical form, since

$$SA^pS^{-1} = (SAS^{-1})^p$$

Suppose that $A \equiv \Sigma A_{ij}$, where A_{ij} are the blocks in the previous appendix. Then, it is sufficient for us to consider one such block A_{ij} of order s. It can be readily shown that

$$(A_{ij})^p = \begin{bmatrix} \lambda^p & \binom{p}{1}\lambda^{p-1} & \binom{p}{2}\lambda^{p-2} & \dots & \binom{p}{s-1}\lambda^{p-s+1} \\ 0 & \lambda^p & \binom{p}{1}\lambda^{p-1} & \dots & \binom{p}{s-2}\lambda^{p-s+2} \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & \lambda^p \end{bmatrix}$$

The elements of this matrix all converge to zero as $p \to \infty$ if and only if $|\lambda| < 1$, if the order of the matrix s is finite.

Hence it follows, that for the full matrix A, $A^p \to 0$ as $p \to \infty$, if and only if all $|\lambda_k| < 1$. Obviously, a diagonalisable matrix is a special case of this. Thus we have

Theorem 4. If the eigenvalues of a matrix A are such that $|\lambda_k| < 1$ for all k, then $A^p \to 0$ as $p \to \infty$. From this it follows that $A^pX \to 0$ as $p \to \infty$ for any arbitrary finite vector X.

The usual proof of this result is based on the expansion theorem, which is however not universally valid.

The proof of the statement that "if any arbitrary vector $X^{(0)}$ is repeatedly multiplied by a matrix, then the process converges to an eigenvector corresponding to the largest eigenvalue λ_1 where $|\lambda_1| > |\lambda_2| \dots > |\lambda_n|$", is quite simple when the expansion theorem is valid. However, a number of interesting problems arise when some of the eigenvalues are repeated. These are discussed below, as also the case when the expansion theorem is not valid.

By repeated multiplication we mean the sequence

$$X^{(p)} = AX^{(p-1)} \text{ so that}$$

$$X^{(p)} = A^pX^{(0)}$$

(a) Suppose the expansion theorem is valid for the matrix A. This is true only if the matrix A is diagonalisable.

Then $X^{(0)} = \sum_1^n \alpha_k X_k$

so that $X^{(p)} = \sum_1^n \alpha_k \lambda_k{}^p X_k$ since $A^p X_k = \lambda_k{}^p X_k$.

Thus $X^{(p)} = \lambda_1{}^p \sum_1^n \alpha_k (\lambda_k/\lambda_1)^p X_k$

As $p \to \infty$, $(\lambda_k/\lambda_1)^p \to 0$ $(k \neq 1)$

and hence $X^{(p)} \to \lambda_1{}^{(p)} \alpha_1 X_1$

If the vector is standardised each time, the process converges to $AX^{(p)} = \lambda_1 X_1$ where X_1 is the standardised form, viz., with the largest component unity.

This result is unique when all the eigenvalues are different. The speed of convergence is geometric with ratio λ_2/λ_1, and if $|\lambda_2| \simeq |\lambda_1|$ this may be very slow.

Suppose, however, that $|\lambda_1| = |\lambda_2|$ but the two are not equal. In particular, when the eigenvalues are real, λ_1 may be equal to $-\lambda_2$. In this case for even iterates

$$X^{(2p)} \to \lambda_1{}^{2p} (\alpha_1 X_1 + \alpha_2 X_2)$$

and for odd iterates,

$$X^{(2p+1)} \to \lambda_1{}^{2p+1} (\alpha_1 X_1 - \alpha_2 X_2)$$

so that after the other eigenvectors have been eliminated, the successive iterates will be alternately parallel to one of the two vectors $\alpha_1 X_1 \pm \alpha_2 X_2$. From $X^{(2p)}$ and $X^{(2p-2)}$, one can get $\lambda_1{}^2$ and $\alpha_1 X_1 + \alpha_2 X_2$. Similarly, from $X^{(2p+1)}$ and $X^{(2p-3)}$, $(\alpha_1 X_1 - \alpha_2 X_2)$ can be obtained, so that X_1 and X_2 can be determined from these. If more than two eigenvalues have their magnitudes equal, the extension is obvious.

On the other hand, suppose λ_1 itself is repeated, e.g., let $\lambda_1 = \lambda_2 = \lambda_3$. In this case, $X^{(p)} \to \lambda_1{}^p (\alpha_1 X_1 + \alpha_2 X_2 + \alpha_3 X_3) = \lambda_1{}^p X'_1$ (say). Since the matrix is supposed to be diagonalisable, there

will be three eigenvectors corresponding to λ_1 and these may be chosen arbitrarily. X'_1 is obviously one of these, and the others may be obtained by keeping the trial vector $X^{(0)}$ orthogonal to this. The process is to be repeated for obtaining the third eigenvector.

(b) Suppose the matrix A is not diagonalisable and so the expansion theorem is not valid. In this case also, it is possible to show that $X^{(p)} = A^p X^{(0)}$ tends to a linear combination of the eigenvectors corresponding to the largest eigenvalues (in a absolute magnitude).

The proof follows from the form of $(A_{ij})^p$ given above, but is omitted as to does not involve any new principle. The authors hope to be able to present the detailed proof of this and other related results elsewhere.

APPENDIX III

The purpose of this appendix is to show that the eigenvalues of the matrix $B = A_1^{-1}A_2$ are all of modulus less than unity if A is positive definite and symmetric.

Let λ_k, X_k be the eigenvalues and the corresponding eigenvectors of the matrix $A_1^{-1}A_2$.

Then
$$A_1^{-1}A_2X_k = \lambda_k X_k \quad \ldots (1)$$

or
$$\tilde{X}_k A_1 A_1^{-1} A_2 X_k = \lambda_k \tilde{X}_k A_1 X_k \quad \ldots (2)$$

or
$$\tilde{X}_k A_2 X_k = \lambda_k \tilde{X}_k A_1 X_k \quad \ldots (3)$$

or
$$\frac{\tilde{X}_k A_2 X_k}{\tilde{X}_k A_1 X_k} = \lambda_k \quad \ldots (4)$$

Since $A = A_1 + A_2$ we have

$$\tilde{X}_k A X_k = (1 + \lambda_k) \tilde{X}_k A_1 X_k \quad \ldots (5)$$

If A is symmetric, and we represent by D the matrix consisting only of the diagonal elements of A, then

$$A_1 - \tilde{A}_2 = D \quad \ldots (6)$$

and $$\tilde{X}_k D X_k = (1-\lambda_k)\tilde{X}_k A_1 X_k \quad \ldots (7)$$

Thus $$\tilde{X}_k A X_k = \frac{(1+\lambda_k)}{(1-\lambda_k)} \tilde{X}_k D X_k \quad \ldots (8)$$

The diagonal elements of a positive definite matrix are all necessarily positive, and so both $\tilde{X}_k D X_k$ and $\tilde{X}_k A X_k$ are positive. It follows that $(1-\lambda_k)/(1+\lambda_k)$ is positive or $-1<\lambda_k<+1$ ... (9)

Since $|\lambda_k|$ are all less than 1, it is obvious that $B^p \to 0$ as $p \to \infty$ so that the GS process would converge when the matrix A is symmetric and positive definite.

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